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# TAXONOMY OF *ERYTHRANTHE* SECT. *MIMULOSMA* (PHRYMACEAE)

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## ABSTRACT

Seventeen species are treated as members of *Erythranthe* sect. *Mimulosma* in North America north of Mexico: *E. ampliata*, *E. arenaria*, **Erythranthe austrolatidens** Nesom, sp. nov. (Baja California Sur), *E. breviflora*, *E. floribunda*, *E. geniculata* (synonym: *Mimulus dudleyi*), *E. hymenophylla*, *E. inflatula* (synonym: *Mimulus evanescens*), *E. inodora*, *E. jungermannioides*, *E. latidens*, *E. moniliformis*, *E. moschata*, *E. norrisii*, *E. patula*, *E. pulsiferae*, and *E. washingtonensis*. The section also is hypothesized also to include one Russian species (*E. stolonifera*) for a total of 18 species. Descriptions, typifications, a key to species, and distribution maps are provided.

**KEY WORDS**: *Mimulus moschatus*, *Mimulus floribundus*, *Erythranthe* sect. *Mimulosma*, *Mimulus moschatus* alliance, Phrymaceae

Sect. *Mimulosma* of the genus *Erythranthe* (formerly part of *Mimulus*; Barker et al. 2012) includes 19 species as treated here, including the widespread *E. moschata* and *E. floribunda*, primarily centered in their native ranges to the western USA. The group has often been referred to as the "*Mimulus moschatus* alliance." Grant (1924) placed these species within her more broadly encompassing *Mimulus* sect. *Paradanthus*.

North American species added here since study of the group by Whittall (1999), Carlson (2002), and Whittall et al. (2006) are *Erythranthe moniliformis*, *E. inodora*, *E. arenaria*, and *E. plotocalyx*. *Mimulus evanescens* proves to have been earlier named as *M. inflatulus* and an earlier name for *Mimulus dudleyi* is *M. geniculatus*. The group also includes one species endemic to southeastern Russia.

The taxonomy of sect. *Mimulosma* (as "the *Mimulus moschatus* alliance") has been studied using pollen morphology (Argue 1980, 1986), vegetative and reproductive morphology (Carlson 2002), and molecular data (Whittall 1999; Whittall et al. 2006). Molecular data show the group to be distinct, but Carlson was unable to find any morphological synapomorphies for it and described it as a "morphologically cryptic clade." Within *Erythranthe*, species of the group are generally recognized by their herbaceous habit, yellow corollas, equal to subequal calyx lobes, and glandular vestiture. Carlson (2002) noted that "traits ... associated with most ingroup species include a tetraploid chromosome number (N = 16), progressively bifurcated stem architecture, viscid herbage, anthers that open completely, and unequal theca."

Most resolutions of molecular and morphological phylogenies divide the species of *Erythranthe* sect. *Mimulosma* between two main groups — a northern group (the "Columbia River clade"; see Maps 1 and 2) and a more southern group (the "Sierra Nevada clade). The latter includes *E. floribunda*, *E. geniculata*, *E. norrisii*, *E. arenaria*, *E. moschata*, *E. inodora*, and *E. moniliformis*. The Columbia River clade includes *E. ampliata*, *E. patula*, *E. hymenophylla*, *E. jungermannioides*, *E. washingtonensis*, and *E. breviflora*. *Erythranthe ampliata*, *E. patula*, and *E. hymenophylla* are a subgroup, the "Snake River clade," within the northern group. The positions of *E. latidens* and *E. pulsiferae* are equivocal; *E. plotocalyx*, first described here, appears to be similar to *E. latidens*.

*Erythranthe inflatula* is hypothesized to be of hybrid origin between *E. latidens* and *E. breviflora*. The Russian *E. stolonifera* apparently is most closely related to *E. moschata-moniliformis-inodora*. Species not included in earlier studies are interpolated here on the basis of morphology and geography.

This account is based primarily on study of collections from ARIZ, BRIT-SMU-VDB, DAV, MO, ND-Greene, NMC, PH, SRSC, TEX-LL, UC-JEPS, and UT. Specimens are cited only for some of the species or variants that have not been generally recognized, but collections at herbaria above have been annotated in documentation of the concepts.

**ERYTHRANTHE** sect. **MIMULOSMA** Nesom & Fraga, Phytoneuron 2012-n: 0. 2012.
**TYPE**: *Erythranthe moschata* (Douglas ex Lindl.) Nesom

**Annuals** and fibrous-rooted or taprooted or **perennials** from rhizomes; vestiture of gland-tipped hairs, varying from minutely stipitate-glandular to villous-glandular, sometimes aromatic. **Leaves** pinnately or subpinnately to palmately veined. **Calyces** strongly ridge-angled to wing-angled at maturity, lobes mostly of equal or subequal length. **Corollas** yellow or white to pinkish or flesh-colored, strongly bilabiate to weakly bilabiate or nearly regular; palate puberulent to short-villous with stiff, usually clavate hairs. **Anthers** included. **Capsules** included (often slightly exserted in *E. norrisii*). Base chromosome number, x = 8.

Two pollen types were recognized by Argue (1980, 1986) among species of sect. *Mimulosma*. All pollen is tricolporate with multiple, elongate endoapertures. Those with the sexine 2 configuration predominantly microreticulate without supramurial granules or spinules are type IIb: *Erythranthe arenaria*, *E. geniculata*, *E. floribunda*, and *E. moniliformis* (presumably *E. norrisii*, which was not sampled, also has type IIb). The others (including *E. moschata*), with supramurial granules or spinules, are type IIc.

An autogamous mating system has evolved independently several times within *Erythranthe* sect. *Mimulosma*. Floral characters associated with a shift from allogamy to autogamy include decreased bilateral symmetry, less reflexed upper corolla lobes, and reduced overall corolla length (with corresponding reduction of anther/stigma separation). Carlson (2002) and Whittall et al. (2006) discussed the evolution of this syndrome and observed that it characterizes *E. floribunda*, *E. patula*, *E. breviflora*, *E. inflatula*, and *E. latidens* and it is noted here that similar features characterize *E. plotocalyx*.

## Key to the American species

1. Plants from rhizomes and/or stolons.

2. Calyx lobes 1–2 mm, apices rounded to mucronate; anthers glabrous; styles scabrous; stolons forming overwintering turions; plants characteristically of cliff faces.
..... **1. Erythranthe jungermannioides**
2. Calyx lobes 2–9 mm, apices acute or acuminate; anthers glabrous or pubescent; styles glabrous; stolons without turions; plants usually of habitats other than cliff faces.

3. Stems erect to ascending-erect; leaves often congested ..... **10. Erythranthe moniliformis**
3. Stems procumbent to decumbent or decumbent-ascending; leaves distinctly separated.

4. Cauline leaves all petiolate, blades (10–)15–40(–50); fruiting pedicels (7–)10–25(–40) mm; calyx lobes triangular to linear-lanceolate or narrowly triangular-acuminate, 2–4 mm; corolla tube-throats 11–16 mm; anthers glabrous to subglabrous . **9. Erythranthe moschata**
4. Cauline leaves usually sessile (proximal sometimes short-petiolate or subpetiolate), blades generally oblong-lanceolate, 30–70 mm; fruiting pedicels (15–)22–50 mm; calyx lobes linear-lanceolate to narrowly triangular with linear-acuminate apices, 5–9 mm; corolla tube-throats 15–18 mm; anthers strongly to weakly hirsute-hirtellous ..... **11. Erythranthe inodora**

1. Plants fibrous-rooted or taprooted, without rhizomes or stolons.

5. Cauline leaves gradually petiolate to sessile or subsessile, blades generally elliptic to lanceolate-elliptic or ovate-elliptic with an attenuate base, palmately 3–5-veined.

6. Stems and pedicels villous-glandular with gland-tipped hairs 0.2–1(–1.5) mm.

7. Corolla tube-throats 9–12(–14) mm, red spots of lower lip conspicuous; calyx prominently red-dotted ..... **13. Erythranthe arenaria**
7. Corolla tube-throats 5–6 mm, red spots of lower lip small and indistinct; calyx commonly without red dots

8. All leaves petiolate; erect to decumbent, sometimes procumbent-trailing, branching at proximal to distal nodes ..... **14. Erythranthe floribunda** (in part, in Arizona)
8. Medial to distal cauline leaves sessile; stems erect to erect-ascending, mostly branched at the base ..... **15. Erythranthe austrolatidens**

6. Stems and pedicels subglabrous to sessile-glandular or minutely stipitate-glandular with gland-tipped hairs 0.1–0.3 mm, without villous hairs.

9. Petioles 2–9 mm, distinctly 3-nerved (winged); fruiting pedicels 12–38 mm, divergent-arcuate ..... **12. Erythranthe pulsiferae**
9. Petioles absent or 1–3 mm, 1-nerved; fruiting pedicels 5–28 mm, straight.

10. Fruiting calyces minutely stipitate-glandular, 8–12 mm; fruiting pedicels 11–28 mm; corolla tube-throats 5–6(–8) mm; leaves basal and cauline ..... **8. Erythranthe latidens**
10. Fruiting calyces sparsely and minutely hirtellous, eglandular or sparsely sessile-glandular, 5–6 mm or 7–11 mm; fruiting pedicels 5–11 mm or 7–18 mm; leaves mostly cauline (basal deciduous by flowering).

11. Fruiting calyces 5–6 mm; fruiting pedicels 5–11 mm; corolla tube-throats 3.5–5 mm, not exserted beyond the calyx margin; all leaves short-petiolate
..... **6. Erythranthe breviflora**
11. Fruiting calyces 7–11 mm; fruiting pedicels 7–18 mm; corolla tube-throats 5–6(–8) mm, exserted 1–3 mm beyond calyx margin; midcauline and distal leaves subpetiolate to subsessile..... **7. Erythranthe inflatula**

5. Cauline leaves abruptly and distinctly petiolate, blades generally ovate with a rounded to truncate or cordate base; palmately or pinnately veined.

12. Stems prostrate to ascending-erect, sharply bent at the basal nodes; fruiting pedicels divergent at ca. right angles from the stem, often closely paired; calyx lobes ovate-rounded
..... **3. Erythranthe hymenophylla**

12. Stems erect to prostrate, decumbent, or ascending, straight (if erect) or geniculate at nodes; fruiting pedicels suberect to ascending-erect, not paired; calyx lobes acute to deltate or shallowly deltate-subulate.

13. Stems and pedicels stipitate-glandular (gland-tipped trichomes unicellular, 0.05–0.2 mm long); leaf blades palmately veined.

14. Corollas regular to weakly bilabiate, tube-throats 7–8 mm **4. Erythranthe patula**
14. Corollas strongly bilabiate, tube-throats 8–12(–14) mm.

15. Stems, leaves, and calyces villous-glandular with vitreous, flattened, multicellular, gland-tipped hairs 0.1–0.8 mm long, leaves densely hairy; stems terete; styles hispid-hirtellous ..... **2. Erythranthe washingtonensis**
15. Stems, leaves, and calyces minutely sessile to subsessile glandular with gland-tipped hairs 0.05–0.2 mm long, leaves very sparsely glandular; styles glabrous; stems 4-angled ..... **5. Erythranthe ampliata**

13. Stems and pedicels villous-glandular (gland-tipped trichomes multicellular, mostly 0.5–1.2(–2) mm long); leaf blades pinnately to subpinnately veined.

16. Plants mostly erect to ascending-erect; calyces greenish; styles hispid-hirtellous; Oregon and Washington ..... **2. Erythranthe washingtonensis**
16. Plants erect to prostrate, decumbent, or ascending; calyces commonly red-spotted; styles glabrous; widespread (15) or California (16, 17).

17. Corolla tube-throats (4–)5–10 mm, limbs expanded 3–4 mm across (pressed) ..... **14. Erythranthe floribunda**
17. Corolla tube-throats 9–11 mm or 12–16 mm, limbs expanded 8–16 mm across (pressed).

18. Calyces with shallowly wing-angled ribs, lobes triangular-acute and erect to spreading or recurving-spreading in fruit; corollas without white patches, tube-throats 9–12 mm, expanded limb ca. 10–18 mm across ..... **16. Erythranthe geniculata**
18. Calyces with rounded-thickened ribs, lobes linear-oblong and incurved in fruit; corollas with white patches on the lower lip, tube-throats 12–16 mm, expanded limb 15–30 mm across ..... **17. Erythranthe norrisii**

1. **Erythranthe jungermannioides** (Suksdorf) Nesom, Phytoneuron 2012-39: 38. 2012. *Mimulus jungermannioides* Suksdorf, Deutsche Bot. Monatsschr. 18: 154. 1900. **TYPE: USA. Washington**. Klickitat Co.: steep, overhanging, damp cliffs near Bingen, Aug-Nov 1892, *W.N. Suksdorf 1470* (holotype: MO!; isotypes: F, NY digital image!, UC!, US digital image!, WTU).

**Perennial**, from thin, above-ground stolons or runners that form terminal bud-like structures (overwintering turions). **Stems** decumbent to procumbent, 5–38(–60) cm, simple or branching near the base. **Stems and pedicels** densely glandular-villous with gland-tipped hairs 0.5–1.2(–1.5) mm. **Leaves** cauline, basal not persistent, blades broadly ovate to broadly lanceolate, 7–35(–40) mm x 8–25 mm, subpalmately to pinnately veined, margins sharply and irregularly dentate to denticulate, apex acute to obtuse, base rounded; petioles mostly 2–5(–20) mm. **Fruiting calyces** cylindric-urceolate, 6–12 mm, plicate-angled, weakly inflated, glandular-villous, lobes subequal, 1–1.5 mm, rounded-

acuminate, suberect, ciliate. **Fruiting pedicels** 15–35 mm. **Corollas** yellow with scattered red spots and two white patches at the tips of the palate ridges, strongly bilabiate, tube-throats funnelform, (12–)16–20(–24) mm, limbs expanded 8–10 mm (pressed), lobes obovate-oblong, apex rounded to truncate. **Styles** scabrous. **Anthers** glabrous. **Capsules** elliptic-lanceolate, 5–9 mm. $2n = 32$. Map 1.

Flowering May–Jul(–Aug). Basalt crevices in seepage zones in vertical cliff faces and canyon walls, within xeric sagebrush communities; 100–400(–1200) m; Oreg., Wash. The record on Map 1 for Jefferson Co., Oregon, is added from OBIC (2011). The Klickitat Co., Washington, occurrence is termed "historical" by WNHP (2005), which also notes that "A sighting of the plant on the WA side was made in the early 1990s, but the location and presence of the species need to be confirmed."

Molecular data place *Erythranthe jungermannioides* and *E. washingtonensis* as sister species.

**2. Erythranthe washingtonensis** (Gandoger) Nesom, Phytoneuron 2012-39: 39. 2012. *Mimulus washingtonensis* Gandoger, Bull. Soc. Bot. France 66: 218. 1919. **TYPE: USA. Washington.** Klickitat Co.: low sandy banks of the Columbia, Bingen, Oct-Nov 1885, *W.N. Suksdorf 560* (holotype: LY; isotypes: CAS digital image!, CU, DS digital image!, GH, MO 2 sheets!, ND-Greene!, NY 2 sheets digital images!, ORE digital image!, OS digital image!, PH!, UC 2 sheets!, US digital image!, WS, WTU).

Printed labels by Meinke in 1987 on type specimens give this: "ISOTYPE of *Mimulus washingtonensis* Gandoger, according to number only; … The numerous sheets distributed under no 560 collectively represent a hybrid swarm of undetermined parentage, probably involving *M. washingtonensis*, *M. patulus*, and *M. floribundus*." Meinke did not provide document to substantiate his observation. Among the plants I have studied of the type collection, density of villous hairs near the stem bases and on the leaf blades varies, and one of the 16 individual plants on the two UC sheets has minutely hirtellous lower cauline vestiture, but all plants I have seen of the type collection have villous-glandular leaf surfaces, which distinguishes them from *E. ampliata*. Matt Carlson (pers. comm.) also notes that he finds the vestiture of the type collection uncharacteristic of the species in its wider occurrence, but whether this has resulted from hybridization is not evident.

**Annuals**, fibrous-rooted or filiform-taprooted. **Stems** erect to ascending, 5–25 cm, often many-branched, terete. **Stems and pedicels** puberulent-glandular to villous-glandular with gland-tipped hairs 0.1–0.8 mm, hairs sometimes vitreous, flattened, and distinctly multicellular. **Leaves** cauline, basal not persistent, blades deltate or ovate to ovate-lanceolate, 4–16(–23) mm x 2–11(–16) mm, palmately veined, margins denticulate to entire, apex acute, base rounded to cuneate or truncate, petioles 2–14 mm. **Fruiting calyces** tubular, 6–8 mm, ridge-angled, weakly inflated, densely and minutely stipitate-glandular, lobes subequal, 0.8–1.2 mm, shallowly deltate, suberect, ciliate. **Fruiting pedicels** 20–50 mm, divergent at nearly right angles. **Corollas** yellow with small reddish brown dots and two white patches on the lower lip, strongly bilabiate, tube-throats funnelform, 8–10 mm, limbs spreading 7–10 mm (pressed), lobes obovate-oblong, apex rounded to rounded-cuneate. **Styles** hispid-hirtellous. **Anthers** glabrous. **Capsules** ellipsoid to ellipsoid-fusiform, 5–8.5 mm. $2n = 32$. Map 1.

Flowering May–Sep. Shallow basalt gravels in narrow channels and intermittent streams, sandy stream banks, open slopes, rocky shelves near seeps; 700–1300 m; Oreg., Wash.

Despite the implication of the epithet, except for the type collection *Erythranthe washingtonensis* occurs most abundantly in the John Day River drainage of eastern Oregon.

**3. Erythranthe hymenophylla** (Meinke) Nesom, Phytoneuron 2012-39: 38. 2012. *Mimulus hymenophyllus* Meinke, Madroño 30: 147, plate 1. 1983. **TYPE: USA. Oregon**. Wallowa Co.: E side of Horse Creek, ca. 12 km S of the Imnaha River and ca. 21 km W of the Snake River, 1075 m, 2 Jul 1980, *R.J. Meinke & Kennison 2656* (holotype: OS digital image!; isotypes: ID, NY digital image!, ORE digital image!, UC!, US digital image!, WS, WTU).

**Annual**, filiform-taprooted. **Stems** prostrate to ascending-erect, 5–25 cm, simple or few-branched. **Stems and pedicels** glandular-puberulent to glandular-villous with vitreous, flattened, multicellular, gland-tipped hairs 0.1–0.8 mm, all hairs glandular. **Leaves** basal and cauline, largest at midstem, blades broadly lanceolate to ovate, 10–35 mm x 10–30 mm, pinnately veined, distinctly membranous, margins coarsely dentate to shallowly denticulate or entire, apex acute to obtuse, base cuneate to shallowly cordate, petioles 6–30 mm. **Fruiting calyces** tubular-campanulate, angled, 5–7 mm, slightly inflated, sparsely stipitate-glandular, lobes subequal, 0.5–1.2 mm, ovate-rounded, suberect, ciliate. **Fruiting pedicels** 10–45 mm, negatively phototropic, causing the capsules to be pressed against the cliff face or into a crevice by the time of dehiscence. **Corollas** light yellow with red or purple spots on the throat and lower lobes, sometimes with small white patches, weakly bilabiate, tube-throats funnelform, 10–14 mm, lobes obovate-oblong, apex rounded to truncate or notched. **Styles** glabrous. **Anthers** glabrous. **Capsules** ovoid, 3–6 mm. $2n = 32$. Map 1.

Flowering Apr–Aug(–Sep). Steep, seasonally moist basalt cliffs with W or SW exposure, within mesic coniferous forests; 800–1300 m; Idaho, Mont., Oreg.

Until recently, *Erythranthe hymenophylla* has been thought to be restricted to deep canyons of Horse Creek and Cow Creek in southeast Wallowa County, Oregon. The Oregon Biodiversity Information Center (2010) notes that the species also is known in Idaho and Montana — county records are added from BONAP (2011).

Meinke (1983) observed that plants of *E. hymenophylla* have reflexed ("strongly negatively phototropic") fruiting pedicels that increase seed dispersal back onto the vertical cliff wall, the characteristic habitat of the species. The "hanging" habit of *E. hymenophylla* is reflected in a sharp (90°–180°) bend in the basal nodes and the long pedicels that are closely paired and divergent in parallel at about right angles from the stem. The species also is characterized by it very short calyx to corolla length, relatively short capsules, and very large seeds.

**4. Erythranthe patula** (Pennell) Nesom, Phytoneuron 2012-39: 39. 2012. *Mimulus patulus* Pennell, Proc. Acad. Natl Sci. Philadelphia 99: 162. 1947. **TYPE: USA. Washington**. Whitman Co.: Wawawai, along irrigation ditches, May 1897, *A.D.E. Elmer 752* (holotype: PH!; isotypes: MO-2 sheets!, SMU!, US digital image!).

**Annuals**, fibrous-rooted or filiform-taprooted. **Stems** erect to ascending, (3–)5–15(–24) cm, usually simple. **Stems and pedicels** stipitate-glandular with gland-tipped hairs 0.2–0.5 mm. **Leaves** cauline, basal not persistent, blades deltate or ovate to ovate-lanceolate, 4–12(–17) mm x 3–10(–14) mm, palmately 3-veined, margins usually denticulate, apex acute to obtuse, base rounded to cuneate-truncate, petioles (5–)8–25 mm. **Fruiting calyces** tubular, 5–6(–7) mm, not inflated or weakly so, sparsely stipitate-glandular to sparsely hirtellous, lobes subequal, 0.7–1.1 mm, deltate, suberect, ciliate. **Fruiting pedicels** 10–25(–38) mm. **Corollas** yellow, usually with a few red or brownish dots on lower lip, regular to very weakly bilabiate, tube-throats funnelform, 7–8 mm, lobes oblong, apex rounded to truncate. **Styles** glabrous. **Anthers** glabrous. **Capsules** ellipsoid to narrowly obovoid, 4–6 mm. $2n = 32$. Map 1.

Flowering Apr–May(–Jul, –Aug). Ephemeral seeps, springs, rocky stream banks, moist basalt, fine gravel on top of bedrock, muddy hillside seeps, crevices; 200–1900 m (–2900 m in Montana and Wyoming); Alberta; Idaho, Mont., Oreg., Wash., Wyo.

*Erythranthe patula* is distinctive in its long-petiolate leaves with ovate blades and its small, weakly bilabiate to nearly regular corollas.

In his dissertation, Meinke (1992) proposed to recognize *Mimulus patulus* "var. montanus," characterized by a cauline vestiture of a mixture of stipitate-glandular hairs and minute (0.1–0.2 mm), sharp-pointed eglandular hairs and with a geographic distribution considerably beyond the typical expression in its range of two or three counties at the corner of eastern Oregon and Washington. The vestiture of typical *Mimulus patulus* is constituted only by minute, stipitate-glandular hairs. "Var. montanus" was not mentioned again in later publications of which Meinke was author or coauthor (Meinke 1995; Whittall et al. 2006) and the MO specimen cited as an isotype of "var. *montanus*" cannot be located at MO or UC.

In any case, intergrades between the two vestiture types appear to indicate that the vestiture is variable within a single species. Meinke (1992) noted that a collection from Wallowa Co., Oregon (*Peck 18282*, NY, WILLU) included plants of both var. *patulus* and var. *montanus*. A collection from Idaho Co., Idaho (*Gray 5571*, MO), might also be interpreted as a mixed collection in the same way. Plants of other collections in 2009 by Karen Gray (MO) from Nez Perce and Idaho counties, Idaho, have stipitate-glandular pedicels but hirtellous, eglandular stems. Collections from Teton Co., Wyoming, have stipitate-glandular stems and pedicels but hirtellous calyces (*Payson & Payson 2226*; *Williams 875*; *Williams 992*; all MO) and would strictly be identified as var. *patula*. *Anderson 366* (UC) from Teton Co. has sparsely glandular calyces. Analogous variation in vestiture occurs among populations of *Erythranthe breviflora* as well as in *E. guttata* (Fischer ex DC.) Nesom of sect. *Simiolus* (Nesom 2012).

**5. Erythranthe ampliata** (A.L. Grant) Nesom, Phytoneuron 2012-39: 38. 2012. *Mimulus ampliatus* A. L. Grant, Ann. Missouri Bot. Gard. 11: 214. 1924. **TYPE: USA. Idaho**. Nez Perce Co.: about Lake Waha, 2000-3500 ft, 27 Jun 1896, *A.A. and E.G. Heller 3330* (holotype: MO!; isotypes: JEPS, MO!, ND-Greene!, UC). The original labels were distributed with a handwritten identification of "Mimulus longipedunculatus Heller, n. sp.," but that name was never published.

**Annuals**, fibrous-rooted or filiform-taprooted. **Stems** erect to ascending, 5–17 cm, often many-branched, 4-angled. **Stems and pedicels** sessile- to subsessile-glandular with gland-tipped hairs 0.05–0.2 mm. **Leaves** cauline, basal not persistent, blades broadly ovate to lanceolate, 8–25 mm x 5–19 mm, palmately veined, margins dentate to coarsely denticulate, apex acute to obtuse, base cuneate, petioles 8–20 mm. **Fruiting calyces** tubular-campanulate, 6–8 mm, not inflated or weakly so, minutely sparsely stipitate-glandular to glabrous, lobes subequal, triangular-acute, suberect, ciliate. **Fruiting pedicels** 10–22 mm. **Corollas** deep yellow with a few brownish dots on the lower lip, sometimes with small white patches, strongly bilabiate, tube-throats broadly funnelform, 8–12(–14) mm, lobes obovate-oblong, apex rounded to truncate. **Styles** glabrous. **Anthers** glabrous. **Capsules** fusiform to narrowly ellipsoid, 5–6 mm. Chromosome number unknown. Map 1.

Flowering Jun–Jul. Basalt outcrops, seepy roadcuts, grassland seeps; 900–1700 m; Idaho (Nez Perce and Idaho counties).

Meinke referred to *Mimulus ampliatus* as a variety (1992) or subspecies (1995) of *M. washingtonensis*, but he apparently never made the formal combination. As understood here, *Erythranthe ampliata* and *E. washingtonensis* have disjunct geographic distributions and are non-intergrading in morphology (as in the key). The geography and vestiture of *E. ampliata* are more similar to *E. patula* than to *E. washingtonensis*.

6. **Erythranthe breviflora** (Piper) Nesom, Phytoneuron 2012-39: 38. 2012. *Mimulus breviflorus* Piper, Bull. Torrey Bot. Club 28: 45. 1901. **TYPE: USA. Washington**. Whitman Co.: Pullman, 3 Jul 1894, C.V. *Piper 1858* (holotype: WS; isotypes: OS digital image!, UC, US digital image!).

**Annuals**, shallowly fibrous-rooted. **Stems** ascending, 4–15 cm, branched at lower and middle nodes. **Stems and pedicels** (and leaves) minutely stipitate-glandular with gland-tipped hairs 0.1–0.3 mm, without villous hairs, sometimes minutely hirtellous with minute-sharp-pointed eglandular hairs (as in *E. patula*). **Leaves** mostly cauline (basal mostly deciduous by flowering), blades narrowly ovate or narrowly lanceolate to elliptic or elliptic-lanceolate, largest mostly 5–15 mm x 2–6 mm, relatively even-sized, or slightly reduced distally, palmately 3-veined, margins entire to mucronulate or denticulate, apex acute to obtuse, base attenuate, narrowed to short (1–3 mm) petiolar regions or subpetiolate to subsessile. **Fruiting calyces** campanulate becoming ovoid-ellipsoid to campanulate, 5–6 mm x 3.5–6 mm, winged and plicate-angled, distinctly inflated, sparsely and minutely hirtellous, eglandular or sometimes sparsely sessile-glandular, lobes subequal, 0.5–1 mm, ovate-deltate, suberect, ciliate. **Fruiting pedicels** 5–11 mm, straight. **Corollas** yellow, spotted or striped, tube-throats cylindric to narrowly funnelform, 3.5–5 mm, not exserted beyond the calyx rim, limb weakly bilabiate, barely widened, lobes broadly obovate, apex rounded. **Styles** glabrous. **Anthers** glabrous. **Capsules** oblong-ovoid to ovoid-cylindric, 4–6 mm. Chromosome number unknown. Map 2.

Flowering May–Jul. Stream and lake sides, gravel bars, springs, moist slopes, damp swales between dunes, along trails; 1000–2300 m; British Columbia; Calif., Idaho, Mont., Nev., Oreg., Wash.

Voucher specimens for range extremities. **British Columbia**. 21.5 mi by road on Rossland-Cascade road from junction near Rossland, occasional on rocky, grassy, S-facing slopes, 4250 ft, 5 Aug 1953, *Calder and Saville 11483* (UC). **Nevada**. Humboldt Co.: Santa Rosa Mts., Martin Creek, moist seep under Veratrum, 7500 ft, 25 Jul 1940, *Munz 16152* (UC).

7. **Erythranthe inflatula** (Suksdorf) Nesom, Phytoneuron 2012-39: 38. 2012. *Mimulus inflatulus* Suksdorf, Werdenda 1: 38. 1927. **TYPE: USA. Washington**. Klickitat Co.: In cultivation at Bingen, "25 May 1901—10 Jun 1903," *W. Suksdorf 9916* (possible holotype: WS; duplicates: MO!, UC!). MO and UC sheets were annotated as 'isolectotype' by R.J. Meinke in 1987.

The type sheet of *Mimulus inflatulus* at MO was identified by annotation by R.J. Meinke in 1987 as *Mimulus breviflorus* subsp. *robustus* Meinke (an unpublished name). He annotated a collection from Harney Co., Oregon (*M.E. Peck 21389*, NY digital image!) as "isotype" of *Mimulus brevifolius* var. *robustus*. Neither *M. inflatulus* nor the name "subsp. robustus" was mentioned in subsequent publications by Meinke (1995a, 1995b, 2007).

*Mimulus evanescens* Meinke, Great Basin Naturalist 55: 250, plate 1. 1995. **TYPE: USA. California.** Lassen Co.: 20.5 km E of Adin, N side of Ash Valley Rd., ca 0.1 km E of the Lassen National Forest boundary, in broken boulders and heavy gravel abutting Moll Reservoir, ca 1500 m, 27 Jun 1990, *R.J. Meinke & T. Kaye 5900* (holotype: OS; isotypes: MO, NY, RM, UC, US, UTC). Deposition of types is as cited by Meinke but judging from their absence on online databases associated with those herbaria, it would seem that none of the specimens have been distributed. Close study of North American *Mimulus* sensu lato at MO and UC did not bring a duplicate of 5900 to light. A topotype has been studied (*Schoenig 98-70*), as cited below).

**Annuals**, fibrous-rooted or filiform-taprooted. **Stems** erect to ascending, 6–20(–25) cm, simple or branched at lower and middle nodes. **Stems and pedicels** (and leaves) minutely stipitate-glandular with gland-tipped hairs 0.1–0.3 mm, without villous hairs. **Leaves** mostly cauline (basal mostly deciduous by flowering), blades narrowly ovate or narrowly lanceolate to elliptic or elliptic-

lanceolate, largest 8–18(–30) mm x (1–)3–7 mm, relatively even-sized, or slightly reduced distally, palmately 3–5-veined, margins entire to mucronulate or denticulate, apex acute to obtuse, base attenuate to obtuse or rounded, narrowed to short (1–3 mm) petiolar regions on proximal, mostly subpetiolate to subsessile distally. **Fruiting calyces** campanulate, maturing ovoid-ellipsoid to campanulate or broadly urceolate, 7–11 mm x 5–6 mm, winged and plicate-angled, distinctly inflated, sparsely and minutely hirtellous, eglandular, lobes subequal, 0.5–1.5 mm, ovate-deltate to broadly triangular, suberect, ciliate. **Fruiting pedicels** 7–18 mm, straight. **Corollas** yellow to pale yellow, sparsely red-spotted or not, tube-throats cylindric, 5–8 mm, exserted 1–2 mm beyond the calyx apex, limb weakly bilabiate, barely widened, lobes broadly obovate, apex rounded or mucronate. **Styles** glabrous. **Anthers** glabrous. **Capsules** oblong-ovoid to ovoid-cylindric or broadly ellipsoid, 5–9 mm. Chromosome number unknown. Map 2. A fuller description is available in Meinke (1995a).

Flowering Jun–Jul. Drying edges, banks, and beds of summer-dry watercourses, near drying edges of small lakes or impoundments, often among rocks and shoreline detritus, occasionally in moist protected areas beneath low shrubs (generally *Artemisia tridentata*), apparently restricted to the ecotone between the upslope edge of the sagebrush-juniper dominated shrub zone and the semi-aquatic graminoids near the water's edge (Meinke 1995a, b); 1200–1700 m. Calif., Idaho, Nev., Oreg. The type collection from Klickitat Co., Washington, was from a cultivated plant — no natural occurrences are known from Washington.

Morphological and molecular data (Meinke 1995a; Beardsley et al. 2004) indicate that *Erythranthe inflatula* originated as a hybrid between *E. breviflora* and *E. latidens*. If so, its geography and biology suggest that it is reproductively stable. The putative parents are geographically and ecologically separated for the most part and the range of *E. inflatula* is considerably broader than the relatively small region where the parents are sympatric. In this region, however, *E. inflatula* may be difficult to distinguish from one or both of its putative parents.

Collections of *Erythranthe inflatula* are these, as cited by Meinke (2007) and with additions from the present study. **California.** Lassen Co.: 7.0 mi N of Madeline, ca. 1 mi N of Sage Hen siding on Southern Pacific RR, ca. 5500 ft, 28 Jun 1957, *Bacigalupi 5989* (JEPS); 3.1 mi S of Madeline, ditches along US Hwy 395, on Madeline Plains, rich, black, peaty soil, 5300 ft, 28 Jun 1957, *Bacigalupi 5998* (JEPS); 10 miles S of Ravendale, 9 Jun 1940, *Pennell 25763* (P); 4.8 miles S of Madeline, 17 Jun 1958, *Raven & Solbrig 13298* (JEPS). Modoc Co.: along Willow Creek, Jun 1894, *Austin s.n.* (UC); SW shore of Moll Reservoir, 2 meters from water's edge, 4920 ft, 5 Jul 1998, *Schoenig 98-70* (DAV, JEPS); Damons Butte, ca. 2.6 mi W of Hwy 139, 4400 ft, cinder cone in a recent lava flow, in *Pinus jeffreyi* woodland with *Artemisia tridentata* understory, site recently burned, dominated by *Ceanothus velutinus*, 4 Jun 1988, *Taylor 9745* (UC). Shasta Co.: ca. 1 mi W of Warner Grade Reservoir, on margins of N-most of four small seasonally inundated ponds, 3030 ft, 14 Jun 1991, *Taylor 11886* (UC). Siskyou Co.: 0.8 mi E of Tennant Rd, NE of Weed, E of Grass Lake and W of Bray on Old State Hwy, ca. 1000 plants in scatteerd groups on a vernally wet, meadowy flat of low scrub, *Oswald & Ahart 9359* (UC). **Idaho.** Owhyee Co.: meadow, 3 mi S of Riddle, 1 Jul 1949, *Holmgren & Holmgren 7973* (CAS, UC, WS, WTU). **Nevada**. Washoe Co.: near CA-NV state line in S end of Coppersmith Hills, clay-loam vernal area with silver sage, *Plagiobothrys*, tansyleaf suncup, 6100 ft, 23 Jun 1986, *Schoolcraft 1635* (UC). **Oregon.** *Crook Co.*: Grizzly Butte, 18 Jun 1894, *Leiberg 275* (NY, ORE, US). Gilliam Co.: forks of Cottonwood Canyon, 6 Jun 1894, *Leiberg 156* (NY, ORE, P, US). Grant Co.: Ochoco National Forest, Graylock Butte, 6 Jul 1912, *Ingram s.n.* (RM). Harney Co.: dry watercourse near Frenchglen, 26 Jun 1942, *Peck 21389* (CAS, NY, P, UC, WILLU) – probably on Burns BLM. Klamath Co.: along the E banks of Dog Hollow Reservoir, 12 Jun 2003, *Meinke s.n.* (OSC); shallow, stony drainage at SE edge of Campbell Reservoir, near culvert, *Meinke s.n.* (OSC) (both sites on Lakeview BLM). Lake Co.: along Dog Creek, W of Drews Reservoir, T. 40. S., R. 17. E., Sec. 11 (NE ¼), 3 Jul 1999, *Meinke s.n.* (donated to Lakeview BLM herbarium; OSC); Sagehen Creek bed, just N of Road 4017 (west of Drews

Reservoir), T. 40. S., R. 17. E., Sec. 1 (SE ¼), 4 Jul 1999, *Meinke s.n.* (donated to Lakeview BLM herbarium; OSC); Whiskey Creek bed, above and below Road 4017 (just W of Drews Reservoir dam and picnic area), T. 40. S., R. 18. E., Sec. 8 (NE ¼), 4 Jul 1999, *Meinke s.n.* (donated to Lakeview BLM herbarium; OSC); along Wool Lake drainage, SE margin of lake, along drying edges and banks of seasonal stream (mixed population with *M. latidens*), T. 38. S., R. 25. E., Sec. 12 (NW ¼), 26 Jun 1999, *Meinke s.n.* (donated to Lakeview BLM herbarium; OSC). Wasco Co.: Near Dalles City, 18 Jun 1901, *Suksdorf 1029* (MO). **Washington**. The collection mapped from Klickitat Co. is the type.

Meinke (2007) knew *Erythranthe inflatula* as represented by only five extant populations or population complexes — in Lassen Co., California, and Klamath and Lake cos., Oregon, but recent collections have substantiated its existence elsewhere and older localities should be revisited toward the possibility that the species persists there. The account of RTE species of Oregon (Oregon Biodiversity Information Center 2010) lists Malheur County in the distribution of the species. Oswald (1992) cited additional collections from Lassen Co., **California**: pool along base of RR, paralleling Poison Lake adjacent to Pittville Rd, *Oswald 5652, 9263* (CHSC).

**8. Erythranthe latidens** (A. Gray) Nesom, Phytoneuron 2012-39: 38. 2012. *Mimulus latidens* (A. Gray) Greene, Man. Bot. San Francisco Bay, 278. 1894. *Mimulus inconspicuus* var. *latidens* A. Gray, Synopt. Fl. N. Amer. (ed. 2) (1, Suppl.): 450. 1886. **LECTOTYPE**: (cited by Grant 1924, p. 202, as "TYPE"): **USA. California.** [Contra Costa Co.:] Near Monte Diablo, 26 May 1862, *W.H. Brewer 1161* (GH?; isotypes: UC!, US digital image!). The protologue gives "On the flanks of Monte Diablo, *Brewer*, *Greene*, and Chollas Valley, San Diego Co., *Orcutt*." The UC sheet is annotated as "Isotype!" by Grant.

Grant (1924) indicated that she saw the Brewer collection at GH but it is not listed on the Harvard University Herbaria website. The specimen currently listed on the website as the type of *Mimulus inconspicuus* var. *latidens* is this: **California**. San Diego Co.: Chollas Valley, San Diego, 20 Jun 1884, *C.R. Orcutt 679* (GH, MO!). An apparent duplicate of the Orcutt collection is at PH, although it has only incomplete collection data. On the Brewer 1161 sheet at UC sheet, Pennell made the following annotation in 1941: "As type of *M. inconspicuus latidens* Gray I take C.R. Orcutt's 479, collected June 20, 1884 at Chollas Valley, San Diego, Calif., since it supplied Gray with most ample material and was his only collection accompanied by dissected flowers in a packet, thus showing its special study by him."

**Annuals**, fibrous-rooted or filiform-taprooted. **Stems** ascending to ascending-erect, 3–10(–25) cm, usually multiply branched from the base. **Stems and pedicels** (and leaves) short-stipitate-glandular to sessile-glandular with gland-tipped hairs 0.1–0.3 mm, without villous hairs. **Leaves** basal and cauline, largest at base or near midstem, sometimes unreduced in size up to the uppermost nodes, cauline blades ovate to ovate-lanceolate, 8–26(–35) mm, palmately 3(–5)-veined, margins entire or barely mucronulate to shallowly dentate-mucronulate, 1–3 teeth or mucronulae per side, apex acute to rounded, base abruptly cuneate to rounded, sometimes subauriculate, petioles absent. **Flowers** (1–)3–12. **Fruiiting calyces** tubular-campanulate, ovoid-ellipsoid, prominently 5-angled, purplish, 8–12 mm x 4–7 mm, strongly inflated, mostly minutely stipitate-glandular, lobes subequal, triangular-acute, suberect, ciliate. **Fruiting pedicels** 11–28 mm. **Corollas** white to pinkish or flesh-colored, rarely yellowish, red-spotted on throat and lower lobes, tube-throats cylindric, 5–6(–8) mm, exserted 1-2 mm beyond calyx margin, limbs nearly actinomorphic, barely widened, lobes broadly obovate, rounded. **Styles** glabrous. **Anthers** glabrous. **Capsules** oblong to oblong-obovoid, 6–7 mm. Chromosome number unknown. Map 2.

Flowering Apr–Jun. Drained flats or slopes subject to vernal inundation, depressions in open fields, bare clay soil, vacant lots, roadsides; 10–800 m; Calif., Oreg.; Mexico (Baja California).

A collection of *Erythranthe latidens* from Madera Co., California, has fruiting calyces 8–12 mm long and variably inflated. The distinction between *E. latidens* and *E. inflatula* sometimes seems arbitrary in northwestern California, where they are sympatric.

9. **Erythranthe moschata** (Douglas ex Lindley) Nesom, Phytoneuron 2012-39: 38. 2012. *Mimulus moschatus* Douglas ex Lindley, Bot. Reg. 13: plate 1118. 1828 [1827?]. *Mimulus guttatus* var. *moschatus* (Douglas ex Lindley) Prov., Fl. Canada 1: 439. 1862. **TYPE: USA. Oregon.** [Multnomah Co.:] Garden specimens grown from seeds collected 'in moist rocks on the Multnomah and the Columbia at the falls of both, 23 May 1825, *D. Douglas s.n.* (holotype: BM?). A specimen at BM (Canada, 1826, *D. Douglas s.n.*, BM digital image!) may prove to be the type but the collection data, as given by BM, do not appear to match the protologue. Lindley wrote that Douglas found it "growing sparingly on the margins of springs in the country about the river Columbia, in North-West America."

*Mimulus crinitus* A.L. Grant, Ann. Missouri Bot. Gard. 11: 186. 1924. *Mimulus acutidens* Reiche, Fl. Chile 6: 63. 1911 (not *M. acutidens* Greene 1885). **TYPE: CHILE.** Prov. Valdivia, en pantanos, *O. Buchtien 159* (holotype: SGO).

*Mimulus leibergii* A.L. Grant, Ann. Missouri Bot. Gard. 11: 231, pl. 6, f. 1. 1924. **TYPE: USA. California.** [Plumas Co.:] Mt. Pleasant, Spanish Peak Range, wet soil along creek, 6500 ft, 16 Jul 1900, *J.B. Leiberg 5171* (holotype: US digital image! photo-MO! photo-UC!).

**Perennials**, rhizomatous, rooting at lower nodes. **Stems** ascending to decumbent or prostrate, 2–30(–40) cm, simple or branched. **Stems and pedicels** glandular-villous with gland-tipped hairs 1–2 mm. **Leaves** cauline, basal not persistent, blades oblong-ovate, (10–)15–40(–50) mm x 5–25 mm, pinnately veined, margins coarsely serrate-dentate to denticulate or subentire, apex acute, base truncate to rounded or subcordate, petioles (1–)2–5(–10) mm. **Fruiting calyces** campanulate, 6–13 mm, weakly inflated or not at all, villous to glandular-villous, plicate-angled, lobes lobes strongly unequal to subequal, 2–4 mm, triangular to linear-lanceolate or narrowly triangular-acuminate, erect to spreading-recurving, ciliate. **Fruiting pedicels** (7–)10–25(–40) mm. **Corollas** mostly yellow with red to blackish or brown lines or red dots or both in the throat on the lobes, weakly bilabiate to nearly regular, tube-throats narrowly funnelform, 11–16 mm, lobes oblong-obovate, apex usually notched. **Styles** glabrous. **Anthers** glabrous to very slightly hirtellous or scabrous. **Capsules** ovoid, 3–7(10?) mm. $2n = 32$. Map 4.

Flowering May–Aug. Shaded and wet places in sagebrush, aspen, spruce-fir, lodgepole pine, and meadows; 1200–3100 m; B.C., Alta., N.B., Nfdl., N.S., Ont., Que., P.E.I.; S.P.M.; [western USA] Calif., Colo., Idaho, Mont., Nev., Oreg., Utah, Wash., Wyo., [eastern USA] Conn., Maine, Mass., Minn., N.H., N.J., N.Y., Penn., R.I., Vt., Va., W.Va., Wis.; introduced: South America (Chile), Europe, Australia, New Zealand, Asia (Japan).

Pennell (1935) noted that the Chilean *Mimulus acutidens* Reiche is the same species as the North American *M. moschatus* and indeed plants from Peru and Chile appear to be inseparable from *M. moschatus* in habit, vestiture, and calyx morphology. Pennell's assessment is corrobated in the present study, based on study of numerous South American collections at MO and UT. Fruiting calyces of the Chilean plants are 6–8 mm, barely expanded from flower; corolla tube-throats 10–12 mm. Von Bohlen (1995b) maintained *Mimulus crinitus* as a distinct species (including *M. acutidens* Reiche as a synonym) but noted that a closer analysis of North American material of *M. moschatus* would be necessary for a better judgement. *Mimulus acutidens* and *M. moschatus* sensu stricto are conspecific.

*Erythranthe moschata* as treated here, recognizing the segregates *E. moniliformis* and *E. inodora*, is narrower in concept than those of recent decades (e.g., Thompson 1993; Carlson 2002; Whittall et al. 2006), where only the single broad species was recognized. Whittall et al. (2006) noted

that "the *Mimulus moschatus* alliance is a group of 13 closely related species with uncertain species boundaries and interspecific relationships (Grant 1924; Pennell 1951; Argue 1986; Meinke 1992; Whittall 1999; Carlson 2002)," but this seems unfair particularly to Pennell, who recognized the two segregates of *M. moschatus* (he also recognized *M. macranthus* as distinct, but it is here regarded as conspecific with *M. moniliformis*). Studies of pollen morphology (Argue 1980, 1986) also explicitly support the segregation of *M. moniliformis* (which has unormamented muri) from *M. moschatus*. Argue's tentative distinction (1980) of the pollen of *M. inodorus* from that of *M. moschatus* was not confirmed in the 1986 study.

In contrast, it seems that neither Meinke nor Whittall nor Carlson has even mentioned the potential existence of the segregates. Munz and Keck (1959) recognized *Mimulus moschatus* var. *moniliformis* as distinct but treated *M. inodorus* as a synonym of *M. moschatus* var. *moschatus*. The only synonym included by Thompson (1993) as a synonym of the broadly conceived *M. moschatus* was "*M. moschatus* var. *moniliformis*."

Each of the three species recognized here (*Erythranthe moschata*, *E. moniliformis*, *E. inodora*, using criteria similar to those of Pennell) has a distinct range but each overlaps with the other two (Maps 3 and 4), and while there are indications that hybrids may be formed, all three apparently maintain their morphological distinction. Zones of intergradation in the areas of overlap are not evident but field studies are needed to examine this more closely.

**10. Erythranthe moniliformis** (Greene) Nesom, Phytoneuron 2012-39: 38. 2012. *Mimulus moniliformis* Greene, Bull. Calif. Acad. Sci. 1: 10. 1884. *Mimulus moschatus var. moniliformis* (Greene) Munz, Aliso 4: 99. 1958. **TYPE: USA. California**. [Kern Co.:] Summit Station, Aug 1883, *E.L. Greene s.n.* (holotype: CAS?; isotypes: GH, MO!). Not located at ND-Greene. Protologue: "Common in dry rocky places of the Sierra, from 4,000 to 8,000 ft. In the collections of Bolander, Kellogg and others, this species occurs abundantly, and is named 'M. moschatus,' being confounded with the last species."

*Mimulus dentatus* var. *gracilis* A. Gray, Bot. Gaz. 7: 112. 1882. **TYPE: USA. California**. [Shasta Co.:] Lassen's Peak, 1882, *Mrs. R.M. Austin s.n.* (holotype: GH). Not located at ND-Greene.

*Mimulus moschatus* var. *sessilifolius* A. Gray, Synopt. Fl. N. Amer. (ed. 2) 2(1): 447. 1886. Gray noted as a synonym "M. inodorus Greene, l.c., but the plant as strongly musk-scented as the ordinary species, at least in some cases." Gray also noted "Not rare in wet places, from San Bernardino Co., California, northward, and passing into the ordinary form in Oregon." **SYNTYPES: USA. California**: Butte Co.: Chico, Apr 1885, *A. Gray s.n.* (GH). **California**. Alameda Co.: Temescal, Tule swamps, Jun 1885, *W.S. Lyon 6* (GH).

*Mimulus moschatus* var. *longiflorus* A. Gray, Synopt. Fl. N. Amer. (ed. 2) 2(1): 278. 1886. Gray noted only "The usual form in California, also in Oregon." In a later citation (p. 447), he noted "M. moniliformis, in part (the villous- and more or less viscous-pubescent plant), Greene, Bull. Calif. Acad. i. 119. Common especially in the Sierra Nevada." **SYNTYPES: USA. California**. Mariposa Co.: Yosemite Valley, 1886, *H.N. Bolander 6306* and *6307* (GH).

*Mimulus macranthus* Pennell, Proc. Acad. Philad. 99: 160. 1947 **TYPE: USA. California**. Shasta Co.: Hatchet Mountain, 6 to 8 mi W of Burney, along stream in coniferous (*Pseudotsuga*) forest, 3900 ft, 7 Jun 1940, *F.W. Pennell 25710* (holotype: PH!).

**Perennials**, rhizomatous. **Stems** erect to ascending, 10–30 cm, simple or usually branched. **Stems and pedicels** (and leaves) densely villous with eglandular or weakly gland-tipped hairs 0.5–2 mm, very rarely glabrate. **Leaves** mostly cauline, basal not persistent, blades oblong-ovate to ovate, 18–40 mm x 7–13 mm, pinnately veined, margins dentate to denticulate, apex acute to obtuse, base rounded to subcordate, subclasping to sessile, petioles absent or 0.5–1 mm. **Fruiting calyces**

cylindric-campanuate, 10–11(–13) mm, weakly inflated, ridged-angled to winged-angled, villous-glandular, lobes subequal, 2–3 mm, lanceolate to triangular-subulate, spreading-recurving, ciliate. **Fruiting pedicels** 10–40 mm. **Corollas** yellow with fine blackish or brownish lines on all sides of the throat, red to brown spots present or not, tube-throats cylindric-funnelform, 12–18 mm, limbs weakly bilabiate to nearly regular, apex rounded. **Styles** glabrous. **Anthers** glabrous, rarely hirtellous. **Capsules** narrowly elliptic-ovoid, 6–8 mm. Chromosome number unknown. Map 4.

Flowering Jun–Aug. Around springs and seeps, creek edges, moist meadows, ditches, along trails, roadsides, rocky ridges, granite outcrops, serpentine talus, fir and pine forests; (1000–)1500–2800 ft; Calif., Oreg.

In his description of *Mimulus macranthus*, Pennell (1947, p. 160–161) noted that "This comprises the major part of the material that has been called *Mimulus moschatus longiflorus* Gray (not *M. longiflorus* (Nutt.) Grant), the remainder being mostly *M. inodorus* Greene. These plants, especially developed in the Cascade Range, and including *M. moniliformis* Greene, have been usually treated as forms of the Musk Flower, *M. moschatus* Dougl., but they seem better considered as distinct species ... ." He recognized both *M. macranthus* and *M. moniliformis*, distinguishing the latter by its "finely pubescent to glabrous leaves" and petiolate leaves. The vestiture proves to be more variable than allowed in Pennell's concept, thus Greene's older epithet has priority for this Sierra Nevada-centered species.

*Mimulus moniliformis* was described by Greene as "Near *M. moschatus*, wholly scentless, villous but scarcely viscid, 3–8 inches high from a perennial root, with subterranean shoots bearing moniliform strings of small tubers." Production of odor has been noted by various collectors and authors to vary in *Erythranthe moschata* and slender "moniliform" rhizomes also are variably produced within the species — neither feature separates *E. moniliformis* from *E. moschata*.

*Erythranthe moniliformis* is distinct from *E. moschata* in its erect habit (vs. decumbent to procumbent in *E. moschata*) and characteristically sessile to subsessile cauline leaves (vs. usually petiolate in *E. moschata*), lending an easily recognizable aspect to the plants. Pedicels of *E. moniliformis* are ascending-erect, while in *E. inodora* and *E. moschata*, both of which are essentially prostrate, pedicels are characteristically spreading at about 90 degrees. Leaves of *E. moniliformis* sometimes are short-petiolate and the distinctions in vestiture and corolla size noted by Pennell (1947) are not consistent. In spite of what may appear to be subtle differences, the two are distinct in geography.

**11. Erythranthe inodora** (Greene) Nesom, Phytoneuron 2012-39: 38. 2012. *Mimulus inodorus* Greene, Bull. Calif. Acad. Sci. 1: 119. 1885. Greene did not cite a type; he referred to "*M. moschatus*, Gray, Bot. Cal. I. 569, not of Dougl. *M. moschatus*, var. *longiflorus*, Gray, Syn. Fl. 278" and noted "Common in both the Coast Range and the Sierra Nevada, throughout California, and also in Oregon." In the Synoptical Flora, Gray noted only "The usual form in California, also in Oregon."

Grant (1924) recognized this entity as *Mimulus moschatus* var. *sessilifolius* A. Gray (with *M. inodorus* as a synonym), here placed as a synonym of *Erythranthe moniliformis*, and noted that it occurs from British Columbia to southern California. She cited numerous specimens but not a type. Pennell (1951) treated it at specific rank, describing its range in California as only in northern counties.

*Mimulus moschatus* var. *pallidiflorus* Suksdorf, Deutsche Bot. Monatsschr. 18: 154. 1900. **TYPE**: **USA. Washington**. Skamania Co.: Springs near Chenowith, 7 Jul 1894, *W.N. Suksdorf 2320* (holotype: ?; isotypes: ORE digital image!, UC, US digital image!).

**Perennials**, rhizomatous, sometimes rooting at lower nodes. **Stems** usually prostrate, sometimes decumbent to ascending, 20–80 cm, few-branched. **Stems and pedicels** (and leaves) villous with eglandular hairs 1–2 mm, sometimes mixed with much shorter stipitate-glandular hairs. **Leaves** cauline, basal not persistent, blades oblong-lanceolate, 30–70 mm x 10–22 mm, pinnately veined, margins denticulate to dentate, apex acute, base rounded, petioles absent or uncommonly with petioles 1–2(–3) mm. **Fruiting calyces** cylindric-campanulate, 10–12 mm, weakly inflated, wing-angled or plicate-angled, glandular-villous with gland-tipped hairs, lobes strongly unequal, 5–9 mm, linear-lanceolate to narrowly triangular with long-acuminate-apiculate apices, spreading, ciliate. **Fruiting pedicels** (15–)22–50 mm. **Corollas** yellow with fine blackish or brownish lines on all sides of the throat, tube-throats narrowly campanulate, 15–18 mm, limbs weakly bilabiate and often nearly regular, apex rounded. **Styles** glabrous. **Anthers** consistently finely hirtellous to hispidulous. **Capsules** 6–8 mm. Chromosome number unknown. Map 5.

Flowering Jun–Sep. Creek banks, gravel bars, flood plains, shallow ditches, swales, damp banks, moist soil in coniferous woods, marshes, bogs, wet sand; 0–1900 m; British Columbia; Calif., Oreg., Wash.

Greene (1885) characterized the species as "Quite distinct from the true musk plant, being of more than twice the size, scentless, and possibly only annual; certainly never rooting at the joints," further noting "villous and slimy but wholly scentless; stems 1–3 feet long, weak and decumbent, but not creeping or rooting; leaves ... closely sessile by a broad base." In contrast to Greene's observation, several collections examined in the present study show that it indeed may root adventitiously at lower nodes.

*Erythranthe inodora* is recognized by its prostrate to decumbent or decumbent-ascending habit, large, mostly sessile leaves, dense villous vestiture, long pedicels, large calyces and corollas, hispid-hirtellous anthers, and particularly by its very long, strongly unequal, linear-triangular calyx lobes. The leaves typically and characteristically are sessile with truncate to rounded or subcordate bases but some are short-petiolate (e.g.: **California**: Lake Co., *Heller 5923*; Siskyou Co., *Heller 7960* and *Oettinger 478*. **Oregon**: Gilliam Co., *Jones 28831*; Jackson Co., *Hammond 312*. **Washington**: Skamania Co., the type of *Mimulus moschatus* var. *pallidiflorus*). In these cases, the distinctive leaf bases, vestiture, calyx morphology, and pubescent anthers are generally diagnostic.

A population system of *Erythranthe inodora*-like plants from counties in southern California probably was the basis for Pennell's attribution (1951) of the species to that area, apparently about 300 miles disjunct from the main range of the species. These plants have the prostrate habit, large leaves, long pedicels, and large corollas of *E. inodora* but the calyx lobes are variable in length and usually do not show the attentuate-apiculate apices characteristic of the latter. Representative specimens: **California**. Los Angeles Co.: Verdugo Canyon, damp woods, 11 Aug 1910, *Blake 1639* (LL); Oak Knoll, Aug 1902, *Braunton 656* (UC). San Bernardino Co., San Bernadino Mts.: marsh, 4000 ft, 21 Jul 1897, *Chandler s.n.* (UC); Lower South Fork Meadow, San Gorgonia Wilderness Area, grassy montane meadow in mixed conifer forest, mostly *Pinus jeffreyi* and *Abies concolor*, ca. 7600-8000 ft, 15 Aug 1976, *Davidson 4713* (UC); 1.2 mi E of Running Springs (town) on Calif. 18, common along seepage in road cut, sandy soil, 6100 ft, 19 Jun 1969, *Holmgren 3596* (UC); Bluff Lake, shade of willows, 7400 ft, 13 Jul 1926, *Munz 10690* (UC); Little Bear Valley, Aug 1884, *Parish 1463* (UC-2 sheets); 1 mi ESE of Jenks Lake, Santa Ana R. drainage, shady creek bed, 7000 ft, 20 Aug 1932, *Wheeler 1158* (UC). San Diego Co.: Palomar Mt., 5500 ft, 7 Apr 1928, *Meyer 504* (UC); Palomar Mt., near Palomar Hotel, 4 Jul 1928, *Meyer 504* (JEPS). Riverside Co.: San Jacinto Mts., Tauquitz Valley, wet meadow, 7500 ft, 8 Aug 1903, Jepson 2300 (JEPS); Hannah's Sawmill, 1/2 mi E of Dutch Flat, edge of stream, ca. 6000 ft, 26 Jul 1928, Meyer 524 (UC 2 sheets); San Jacinto Mts., Tahquitz Valley, on a stream bank, 3 Jul 1928, Meyer 601 (JEPS, UC).

Plants seemingly disjunct inland in Butte Co., California, are otherwise typical of the species. Examples: Butte Co.: Damp sand at S edge of Butte Creek, ca. 2.1 mi S of Skyway and ca. 1/4 mi E of Hwy 99 bridge, 29 Aug 1987, *Castro 213* (DAV); Chico, 28 Jul 1916, *Hazeltine s.n.* (DAV).

**12. Erythranthe pulsiferae** (A. Gray) Nesom, Phytoneuron 2012-39: 38. 2012. *Mimulus pulsiferae* A. Gray, Proc. Amer. Acad. Arts 11: 98. 1876. **LECTOTYPE** (Grant 1924, p. 212): **USA. California**. [Plumas Co.:] Indian Valley, 1873, *Mrs. Pulsifer-Ames 21* (GH). Gray cited "California, in the Sierra and Indian Valleys of the Sierra Nevada, Bolander, Mrs. Pulsifer-Ames." Grant (1924) cited *Ames 21* as the "Type."

**Annuals**, shallowly fibrous-rooted. **Stems** erect, 5–12(–18) cm, simple or sparingly branched at the base. **Stems and pedicels** minutely stipitate-glandular with gland-tipped hairs 0.1–0.3 mm. **Leaves** basal and cauline, blades elliptic-oblong to ovate or oblanceolate, 3–14(–23) mm x 2–9(–15) mm, palmately 3-veined, margins denticulate to entire, apex acute to obtuse, base cuneate to attenuate, petioles 2–9 mm. **Flowers** 1–5. **Fruiting calyces** cylindric, 7–10 mm, weakly to strongly inflated, stipitate-glandular, lobes subequal, 0.9–1.1 mm, triangular-acute, suberect, ciliate. **Fruiting pedicels** 12–38 mm, divergent-arcuate. **Corollas** yellowish, "limb pale yellow with pink edges, throat yellow," "white with yellow throat and pink border to the expanded limb," reddish dots present or not on the lower lip, tube-throats funnelform, 6–9 mm, limbs weakly bilabiate, lobes broadly obovate-suborbicular, apex rounded. **Styles** glabrous. **Anthers** glabrous. **Capsules** fusiform-cylindric, 5–8 mm. $2n = 32$. Map 6.

Flowering Apr–Jul. Damp depressions, moist gravel, rocky flats, granite outcrops, wet meadows, lava beds, vernal pools, forest openings, commonly in or near coniferous forest, also chaparral-live oak; 50–1300(–2500) m; Calif., Oreg., Wash.

*Erythranthe pulsiferae* is characterized by its minutely stipitate-glandular vestiture (lacking villous hairs), elongate internodes, persistent basal leaves, small, palmately veined, short-petiolate cauline leaves with elliptic-oblong to ovate or oblanceolate blades, divergent-arcuate pedicels, and small, weakly bilabiate corollas. *Erythranthe floribunda* is distinct from *E. pulsiferae* in its multicellular vestiture, urceolate fruiting calyces, and pinnately veined leaves with generally deltate to ovate blades and more strongly toothed leaf margins. The vestiture of *E. pulsiferae* is generally more similar to that of the Columbia River clade.

The anther pairs and stigma of *Erythranthe pulsiferae* are at essentially the same level and the species appears to be consistently autogamous over its range. Rare plants in Humboldt County (e.g., *Tracy 7616* and *12838*, JEPS) have slightly longer corolla tube-throats and broader limbs — in these the anther pairs are slightly separated and the stigma is at or slightly above the upper anther pair.

**13. Erythranthe arenaria** (A.L. Grant) Nesom, Phytoneuron 2012-39: 38. 2012. *Mimulus arenarius* A.L. Grant, Ann. Missouri Bot. Gard. 11: 215. 1924 [1925]. **TYPE: USA. California**. Fresno Co.: moist sandy places near Huntingdon Lake, 7000 ft, 5 Jul 1917, *A.L Grant 1032* (holotype: MO!; isotypes: DS, GH, BH, JEPS!, OS digital image!, PH!, POM, RM, US digital image!).

*Mimulus subulatus* (A.L. Grant) Pennell, Proc. Acad. Nat. Sci. Philad. 99: 162. 1947. *Mimulus floribundus* var. *subulatus* A.L. Grant, Ann. Missouri Bot. Gard. 11: 222. 1924. **TYPE: USA. California**. [Tuolumne Co.:] between Hog Ranch and Hetch-Hetchy Valley, 4200 ft, 16 Jun 1917, *A.L. Grant 970* (holotype MO!; isotypes: GH, JEPS!, US digital image!).

*Mimulus multiflorus* Pennell, Proc. Acad. Nat. Sci. Philad. 99: 161. 1947. **TYPE: USA. California**. Fresno Co.: 4 mi E of Dunlop, moist granitic gravelly sand, 3700-3800 ft, 9 Aug 1940, *F.W. Pennell 26451* (holotype: PH!; isotypes: MO!, NY 2 sheets digital images!, US digital image!).

*Mimulus trisulcatus* Pennell, Proc. Acad. Nat. Sci. Philad. 99: 161. 1947. **TYPE: USA. California.** [Tulare Co.:] below Mineral King [western slope], moist gravelly granitic soil, 7000–7600 ft, 6 Aug 1940, *F.W. Pennell 26421* with A. Cronquist (holotype: PH!; isotypes: MO!, NY 2 sheets digital images!, UC!, US digital image!).

**Annuals**, fibrous-rooted or filiform-taprooted. **Stems** erect to ascending, 5–20 cm, simple or branched. **Stems and pedicels** villous-glandular with gland-tipped hairs 0.2–0.8 mm. **Leaves** basal and cauline, blades elliptic to narrowly elliptic, ovate-elliptic, or ovate-lanceolate, 5–12(–17) mm x 3–7 mm, 1-veined or palmately 3-veined, margins entire to sparsely dentate to serrate, apex acuminate to acute or obtuse, base rounded to cuneate-attenuate, petioles essentially absent or proximally 1–3(–5) mm on proximal leaves. **Fruiting calyces** narrowly campanulate 5–7(–9) mm, not inflated or weakly so, often red-dotted, villous-glandular, lobes subequal, ca 1 mm, deltate-subulate to broadly triangular, suberect, ciliate. **Fruiting pedicels** 10–23 mm, divergent-arcuate. **Corollas** yellow with red-mottled lower lip, tube-throats funnelform, 9–12(–14) mm, limbs weakly bilabiate, lobes broadly obovate, apex rounded. **Styles** glabrous. **Anthers** glabrous. **Capsules** elliptic, 4–7 mm. $2n = 32$ (*Heckard 4067*, JEPS). Map 6.

Flowering May–Sep. Sandy flats, bars, gullies, washes, trails, and road cuts, seasonal creek beds and drainages, rocky slopes, seepy loam, ditches, lake edges, meadows, openings in pine-fir and pine-oak woodlands; (100–)500–2600(–2800) m; Calif. (Fresno, Los Angeles, Madera, Mariposa, Tulare, Tulomne).

Most plants of *Erythranthe arenaria* have relatively even-sized cauline leaves, all sessile to subsessile. Some, however, have persistent basal leaves that are short-petiolate, ovate with a cuneate base, and relatively larger than the more distal cauline ones. Such plants are those named by Grant as *Mimulus floribundus* var. *subulatus*. These might be construed as showing influence of *E. geniculata*, but the latter occurs only at the lower range of elevation for *E. arenaria* and the "subulata" variants occur at least up to 2300 meters. The "subulata" variants also have the erect habit characteristic of *E. arenaria*. In any case, these variants should be investigated, especially in the Yosemite area where they appear to be relatively common, toward the possibility that they represent a distinct entity.

It is remarkable that Pennell described two species, based on his own collections and field observations, that appear to be essentially segregates from *Erythranthe arenaria*. Yet there do not appear to be discontinuities in corolla size or morphology, features he emphasized in descriptions of *Mimulus multiflorus* and *Mimulus trisulcatus*. Variability in overall size perhaps contributed toward recognition of *M. multiflorus*. California botanists perhaps will be able to corroborate Pennell's field observations of corolla variation and partition the variation more precisely.

Plants of a collection of *Erythranthe arenaria* from Mariposa County (N of Fish Camp, 4900-5100 m, *Pennell 26392*, UC) have mature calyces conspicuously longer (8–9 mm vs 5–7 mm) and more inflated than characteristic for the species and the corollas are slightly longer. Otherwise, they seem securely identified as *E. arenaria*.

Plants of the apparently disjunct collection from Los Angeles County are similar to those in counties further north: Los Angeles Co.: San Gabriel Mts., upper slopes of Little Rock Creek Canyon, ca. 1 mi W of Cedar Spring, sandy base of scree slope on N face of Kratke Ridge, 6800 ft, 20 Jul 1958, *Bacigalupi 6416* (JEPS).

**14. Erythranthe floribunda** (Douglas ex Lindley) Nesom, Phytoneuron 2012-39: 38. 2012. *Mimulus floribundus* Douglas ex Lindley, Bot. Reg. 13: plate 1125. 1827. **TYPE: USA. Washington**. Protologue: "A neat hardy annual, found by Mr. Douglas on moist rocks in the interior of the districts of the river Columbia" (holotype: K?). Grant (p. 218) noted "on

limestone rocks on dry sandy soils in the interior of the Columbia, 1826, *Douglas* (G, probably part of the type collection)."

*Mimulus peduncularis* Douglas ex Bentham, Scroph. Ind., 29. 1835. **TYPE: USA**. "America boreali-occident," 1826, *Douglas s.n.* (holotype: K, sketch and fragment of type at MO!). The full entry of the protologue is this "21. M. PEDUNCULARIS (Dougl. MSS.), pubescens, humilis, foliis petiolaris ovatis acutis subdentatis basi cuneatis rotundatisve, calycibus (parvis) ovato-tubulosis, dentibus brevibus acutis subqequalibus.— America boreali-occident. *Douglas*." Collected in 1826, *D. Douglas s.n.* (holotype: K, sketch of type at MO).

*Mimulus deltoideus* Gandoger, Bull. Soc. Bot. France 66: 218. 1919. **TYPE: USA. Oregon**. [Lake Co.:] North Pine Creek, near Snake River, moist situations, 13 Jul 1899, *W.C. Cusick 2237* (holotype: ?; isotypes: BH, MO!, OS digital image!, UC!).

*Mimulus serotinus* Suksdorf, Deutsche Bot. Monatsschr. 18:154. 1900. **TYPE: USA. Washington**. Klickitat Co.: damp sandy banks of the Columbia River, Oct-Dec 1892, *W.N. Suksdorf 2185* (holotype: WS; isotypes: DS, MO!, NY digital image!, ORE digital image!, UC 2 sheets!, US digital image!; possible isotype: NY digital image!).

*Mimulus membranaceus* A. Nelson, Bot. Gaz. 34: 30. 1902. *Mimulus floribundus* var. *membranaceus* (A. Nelson) A. L. Grant, Ann. Missouri Bot. Gard. 11: 221. 1924. **TYPE: USA. Wyoming**. [Albany Co.:] Centennial Hills, 16 Jul 1894, *A. Nelson 1683* (holotype: RM; isotypes: BH, GH, MO!, NY digital image!).

**Annuals**, fibrous-rooted or filiform-taprooted. **Stems** 3–22(–40) cm, erect to decumbent, sometimes procumbent-trailing, simple to many-branched. **Stems and pedicels** villous-glandular with gland-tipped hairs greatly variable in length and density, sometimes reduced to sparsely stipitate-glandular with hairs 0.2–0.5 mm. **Leaves** cauline, basal mostly deciduous by flowering, blades ovate, (3–)8–25(–35) mm x (1–)5–18(–26) mm, pinnately to subpalmately veined, margins serrate to sparsely dentate, apex acute, base cuneate to truncate or cordate, petioles 1–12 mm. **Fruiting calyces** cylindric, 4–7 mm, weakly to strongly inflated, greenish or purplish to red-dotted, villous-glandular, lobes subequal, (0.5–)0.8–1.6(–2) mm, triangular-acuminate, suberect, ciliate. **Fruiting pedicels** 5–20(–26) mm. **Corollas** yellow with red-dotted lower lip, tube-throats funnelform-cylindric, (4–)5–10 mm, limbs weakly bilabiate, expanded 3–4 mm across (pressed), lobes mostly oblong, apically notched. **Styles** glabrous. **Anthers** glabrous. **Capsules** obovoid to elliptic, 3.5–7 mm. $2n = 32$. Map 7.

Flowering (Apr– in Arizona, May–)Jun–Aug(–Sep). Under overhangs, moist roofs of cave ruins, wet rock crevices, cliff faces and wet cliff bases, below waterfalls, seeps, springs, humus and moist soil over rocks and slabs, moist slopes, along ditches and pond edges, wet edges of creeks and rivers, drying mud on margins of wetland depressions, creek beds, wet or swampy meadows, along trails, in lodgepole pine, ponderosa pine, ponderosa pine-douglas fir, and spruce-fir woodlands; (1000–)1800–1600(–3100) m (ca. 300–500 m in Arkansas); Alta., B.C.; Ariz., Ark., Calif., Colo., Idaho, Mont., Nev., N.Mex., Oreg., Wash., Utah, S.Dak., Wyo.; Mexico (Baja California, Baja California Sur, Chihuahua, Sinaloa, Sonora).

Collections have been made of plants much reduced in size — in leaves, flowers, and overall stature — so strikingly so that one might suspect that they are evolutionarily distinct, but the sizes appear to be at the lower limits of the species (as in the description above) and such plants are identified here as *Erythranthe floribunda*. The following is an example: **Nevada**. Nye Co.: Toquima Range, Toiyabe National Forest, Pine Creek Canyon, ca. 8500 ft, abundant along small stream, 13 Jul 1964, *Holmgren and Reveal 1444* (TEX).

*Erythranthe floribunda* has been recognized from northern Arkansas (e.g., Moore 1958), where documented from a number of counties (Carroll, Cleburne, Crawford, Franklin, Izzard, Johnson, Logan, Newton, Pope, Searcy, Stone, and Washington). The unpublished name "Mimulus floribundus subsp. moorei Iltis" has appeared in various checklists in reference to the Arkansas plants,

but observations in the current study of populations in the herbarium and field indicate that they are not distinct from the rest of the species. The disjunction in geography appears to be analogous to that in *E. moschata*.

Some plants identified here as *Erythranthe floribunda* in Arizona and southwestern New Mexico (e.g., Figs. 1–3) are distinctive in their prominently inflated calyces, sessile to subsessile leaves with attenuate bases and palmately 3–5-nerved venation, and much-elongated pedicels (20–43 mm), but intermediates in Arizona make it difficult to conclude that the variants represent an entity discontinous from plants of typical morphology. This variant morphology has not been observed among Mexican populations.

Figure 1. *Erythranthe floribunda* variant from Hidalgo Co., New Mexico (one of several plants from *Worthington 32511*, SRSC).

Figure 2. *Erythranthe floribunda* variant from Hidalgo Co., New Mexico (*Todsen s.n.*, NMC).

Figure 3. *Erythranthe floribunda* variant from Williams, Coconino Co. (*Greene s.n.*, ND-Greene).

1. Cauline leaves basally attenuate to sessile or subsessile, epetiolate, blades oblanceolate to elliptic or elliptic-lanceolate, primarily palmately 3–5-nerved, sometimes with an additional 1–2 smaller lateral pairs; fruiting pedicels 20–43 mm; corolla tube-throats 5–6 mm; fruiting calyces 5–8 mm ..... **Arizona/New Mexico variant**

1. Cauline leaves abruptly and distinctly petiolate, blades generally ovate with a rounded to truncate or cordate base; mostly pinnately to subpalmately veined; fruiting pedicels 5–15(–26) mm; corolla tube-throats (4–)5–10 mm, fruiting calyces 4–7 mm ..... **Erythranthe floribunda**

Collections examined of the *Erythranthe floribunda* variant. **Arizona**. Coconino Co.: Williams, wet meadow, 6 Jul 1889, *Greene s.n.* (ND-Greene 2 sheets). Pima Co.: S end of Baboquivari Mts., in sand along edge of Presumido Wash near Buenos Aires, ca. 3000 ft, 3 Apr 1966, *Mason 2559* (ARIZ). Santa Cruz Co.: Meadow Hills Country Club, 4.5 mi N of Nogales, wet soil in marsh, [ca. 3900 ft,] 5 May 1966, *Crutchfield 1460* (LL); Santa Rita Mts., 4500 ft, 17 Apr 1903, *Thornber 505* (UC). **New Mexico**. Hidalgo Co.: 30 mi S of Animas, edges of ponds near Gray's Ranch and sandy banks of Animas Creek, 5000 ft, 19 Jun 1973, *Todsen s.n.* (NMC). Peloncillo Mts., Clanton Draw, 3.0 mi E of the [Coronado] National Forest, E side property line, 5480 ft, annual at edge of stream, 9 May 2004, *R.D. Worthington 32511* (NMC, SRSC, UNM, UTEP).

Previous tentative identifications on the three Hidalgo County sheets include *Mimulus floribundus*, *M.* "probably *floribundus*," *M. primuloides*, and *M. rubellus*. Similar ambiguity in identification of New Mexico collections recently confirmed as *Erythranthe suksdorfii* was noted by Keller (2010), but the New Mexico distribution of this species is north of Hidalgo County and the collections cited by Keller seem securely identified as *E. suksdorfii* (fide Phil Tonne, UNM).

A collection from southwestern Mexico is similar to *Erythranthe floribunda* but it is far-disjunct from other populations of that species, completely prostrate, and has very short pedicels: **Jalisco**. W of San Sebastian, Hacienda del Ototal, wet sand of stream bottom, 1500 m, *Mexia 1853* (UC). Fig. 4. It perhaps belongs with plants named by Bentham as *Mimulus pubescens*, which may prove to be a distinct species.

*Mimulus pubescens* Bentham, Prodr. (DC.) 10: 372. 1835. **TYPE**: **MEXICO. Jalisco**. "In Mexico prope Talisco," *Beechey s.n.* (holotype: K, photo MO!). The only information on the specimen is "Mexico, Beechey." See comments below.

Figure 4. *Erythranthe* from Jalisco, Mexico. Possibly what Bentham meant by *Mimulus pubescens* Benth. See comments below.

**15. Erythranthe austrolatidens** Nesom, **sp. nov. TYPE: MEXICO. Baja California Sur**. Sierra Guadalupe, W of Mulege, W side of the mountain range, vicinity of Rancho El Tule, E of San Martin and La Vinorama, 26° 81' N, 112° 72' W, rocky volcanic substrate, with *Lysiloma candida*, *Opuntia cholla*, *Pachycereus pringlei*, ca. 260 m, 26 Apr 1998, *Rebman 5170* (SD!).

Similar to *Erythranthe latidens* in its annual duration, fibrous roots, yellow, cleistogamous/ autogamous flowers, sessile leaves, tubular campanulate calyces with 5 equal, deltate lobes; different in its short villous-glandular vestiture of stems, leaves, pedicels, and calyces, petiolate proximal leaves, consistently serrulate-denticulate leaf margins, generally smaller fruiting calyces, and disjunct geography in Baja California Sur.

Additional collections examined. **MEXICO. Baja California Sur**. Mpio. Comondú, La Laguna, al norte de San José de Comondú, matorral sarcocaule, 443 m, 26° 06' 48.2" N, 111° 46' 38.2" W, 14 Mar 2002, *Dominguez L. 3136* (ARIZ-2 sheets, SD). Mpio. Comondú, Sierra La Giganta, Llanos de San Julio, 5 km al E de San José de Comondú, matorral xerófilo, 432 m, 19 Feb 2003, *Dominguez L. 3399* (ARIZ). Mpio. de La Paz, Mison de Los Dolores, 3 km al SW del Rancho Los Dolores, 25° 03' 20.8" N, 110° 53' 28.1" W, matorral xerófilo, 85 m, 15 Mar 2003, *Dominguez L. 3448* (SD).

**Annuals**, fibrous-rooted. **Stems** terete, 6–22 cm, nodes 3–5, branched mostly at the base, erect to erect-ascending. **Stems, leaves, pedicels, and calyces** short-villous-glandular with gland-tipped hairs 0.1–1.0 mm, without eglandular hairs. **Leaves** basal and cauline, basal often deciduous by flowering, largest at base or near midstem, cauline blades ovate to elliptic or obovate, 5–25 x 2–11 mm, basal blades to 30 mm long, 15 mm wide, palmately 3–6-veined, often suprabasal, margins consistently serrulate-mucronulate to -denticulate, (2–)4–6 teeth per side, apex sharply acute, base acute to cuneate, basal and lower cauline petiolate with petioles 1–6 mm. **Flowers** 5–13, from basal to distal nodes. **Fruiting calyces** tubular-campanulate, ovoid-ellipsoid, 5 angled, greenish with purple ribs, 8–9 mm x 3–5 mm, slightly inflated, lobes subequal, deltate-rounded, apex apiculate, margins weakly ciliate. **Fruiting pedicels** 5–30 mm. **Corollas** yellow, apparently without red markings, tube-throats cylindric, 7–8 mm, exserted 2(–3) mm beyond calyx margin, limbs nearly actinomorphic, barely widened, lobes obovate, apices rounded. **Styles** glabrous. **Anthers** glabrous. **Capsules** 4–6 mm, oblong to oblong-obovoid, stipitate. Map 3.

Flowering (Jan–)Feb–Apr. Xeric shrubland; ca. 100-250 m; Baja California Sur.

*Erythranthe austrolatidens* is similar to *E. latidens* in its overall aspect, but the differences in vestiture and leaf margins and base are readily apparent. These plants have mostly been identified as *E. floribunda*, to which it may be most closely related, but typical E. floribunda occurs all the way south in Baja California to the Cape Region. The new species is directly contrasted with both in the couplets below.

1. Vestiture villous-glandular, hairs 0.1–1.0 mm; basal and lower cauline leaves petiolate; margins consistently serrulate-mucronulate to serrulate-denticulate, (2–)4–6 teeth per side; fruiting calyces 8–9 mm x 3–5 mm ..... **Erythranthe austrolatidens**

1. Vestiture stipitate glandular, hairs 0.1–0.3 mm; all leaves sessile; margins entire or barely mucronulate to shallowly dentate-mucronulate; fruiting calyces 8–12 mm x 4–7 mm ..... **Erythranthe latidens**

1. Medial to distal cauline leaves sessile; stems erect to erect-ascending, mostly branched at the base ..... **Erythranthe austrolatidens**

1. All leaves petiolate; erect to decumbent, sometimes procumbent-trailing, branching at proximal to distal nodes ..... **Erythranthe floribunda**

**16. Erythranthe geniculata** (Greene) Nesom, Phytoneuron 2011-39: 38. 2011. *Mimulus geniculatus* Greene, Bull. Calif. Acad. Sci. 1: 280. 1885. *Mimulus floribundus* var. *geniculatus* (Greene) A.L. Grant, Ann. Missouri Bot. Gard. 11: 220. 1924. **TYPE**: **USA. California**. Kern Co.: Tehachapi, 1884, *Mrs. Curran s.n.* (holotype: CAS, fragment CAS 290198, fragment MO!; isotype: US digital image!). The CAS website provides this information: "Probably the holotype was lost in the 1906 fire. This [CAS 290198] is a fragment of that HT, returned by Pennell." The MO label (ex CAS) has handwritten "Part of the type."

*Mimulus dudleyi* A.L. Grant, Ann. Missouri Bot. Gard. 11: 235. 1924. **TYPE**: **USA. California.** Tulare Co.: rocky cliffs E of the Tule River, 27 Mar 1897, *W.R. Dudley s.n.* (holotype: DS digital image!).

**Annuals**, fibrous-rooted or filiform-taprooted. **Stems** ascending to decumbent or prostrate, 5–60 cm, simple to diffusely branched. **Stems and pedicels** moderately villous with multicellular eglandular hairs 0.8–2 mm and stipitate-glandular hairs 0.1–0.3 mm. **Leaves** basal and cauline or basal mostly deciduous by flowering, blades broadly ovate or elliptic-ovate to triangular, 8–35 x 5–30 mm, pinnately to subpinnately veined, margins serrate or dentate with 3–10 teeth per side, apex acute to obtuse or rounded, base cuneate to rounded or subcordate, petioles 2–10(–35) mm. **Fruiting calyces** campanulate-cylindric, (5–)6–8 mm, weakly inflated, ridged-angled, red-spotted, sparsely to moderately villous-glandular, lobes subequal, 1–3 mm, deltate to narrowly triangular or triangular-acuminate, usually apiculate or indurate, suberect to spreading-recurving, ciliate. **Fruiting pedicels** 12–26(–55) mm. **Corollas** yellow, red-spotted in throat, spots concentrated or becoming coalescent into a somewhat discrete blotch at the base of each of the 3 lower lobes and sometimes the 2 upper as well, tube-throats cylindric, 9–11 mm, limbs strongly to weakly bilabiate, expanded 8–14 mm across (pressed). **Styles** glabrous. **Anthers** glabrous. **Capsules** obovoid to elliptic, 4–6(–7) mm. 2n = 32 (reported as *Mimulus dudleyi*; *Heckard 4003*, UC). Figs. 5 and 6. Map 8.

Flowering (Mar–)Apr–Jul. Granite crevices, canyon slopes, and talus, crevices in volcanic outcrops (Butte and Tulare cos.), edge of boulders, roadsides, damp sandy soil, sandy water edges, gravelly soil and creek bottoms; 200–900(–1200) m; Calif.

Only a single collection of *Erythranthe geniculata* has been seen in the current study from each of Butte and Stanislaus counties: Butte Co.: North Table Mt., ca. 7 mi N of Oroville, face of basal cliffs on the S side of a small stream, ca. 100 yds S of the fence, ca. 1 mi NW of the parking area, cow chute, and Cherokee Road, basalt grassland, 1241 ft, 3 May 2006, *Ahart 12,563* (UC). Stanislaus Co.: along Hwy 132 ca. 200 yards E of Basso Bridge, 2 mi SW of La Grange, wet soil beside pond, 27 May 1969, *Allen 355* (DAV).

*Erythranthe geniculata*, like *E. arenaria*, has recently been treated as synonymous with *E. floribunda*. The latter, however, has much smaller corollas and is autogamous, while the flowers of *E. geniculata* and *E. arenaria* are larger, chasmogamous, and allogamous. In the original description of *Mimulus geniculatus*, Greene noted that it had corollas twice the size of *M. floribundus*. The anther pairs of *E. geniculata* and *E. arenaria* are at different levels and the stigma is slightly above the upper anther pair, while in *E. floribunda* both anther pairs and the stigma are at the same level.

*Erythranthe geniculata*, *E. arenaria*, and *E. norrisii* constitute a group of apparently closely related species endemic along the Sierra Nevada. All have ovate-petiolate leaves (only the basal are sometimes ovate in *E. arenaria*) with pinnate to subpinnate venation. The more widespread *E. floribunda*, which is part of the group, also is similar but the three endemics have larger corollas with the tube-throats exserted at greater length beyond the calyx margin.

Figure 5. *Erythranthe geniculata*. Granite-Woody Rd., Kern Co., California. Photo by Mark Egger, 3 April 2010.

Figure 6. *Erythranthe geniculata*. Indian Wells Canyon, Kern Co., California. Photo by Naomi Fraga, 15 April 2011

17. **Erythranthe norrisii** (Heckard & Shevock) Nesom, Phytoneuron 2012-39: 39. 2012. *Mimulus norrisii* Heckard & Shevock, Madroño 32: 179. 1985. **TYPE: USA. California.** Tulare Co.: Comb Rocks above Washburn Cove, 2 mi N of Three Rivers, 2800 ft, 1 May 1983, *L.L. Norris 389* (holotype: JEPS!; isotypes: CAS, FSC, K, MO, NY digital image!, RSA).

**Annuals**, fibrous-rooted or filiform-taprooted. **Stems** ascending to erect-ascending, 2–15(–25) cm, commonly branched from lower nodes. **Stems** and **pedicels** villous-glandular. **Leaves** basal and cauline, blades elliptic to elliptic-obovate, 20–35 mm x 10–20 mm, 3–5-palmately veined, sometimes with 1–3 distal vein pairs diverging pinnately, surfaces minutely villous-glandular, margins subentire to distally denticulate, apex acute to obtuse, base mostly attenuate, petioles 5–10(–15) mm. **Fruiting calyces** campanulate, 4–6 mm, weakly inflated, villous-glandular, sulcate between rounded and thickened ribs, lobes subequal, 1.5–2 mm, linear-oblong to oblong-lanceolate with rounded to blunt apices, often incurved, villous. **Fruiting pedicels** 20–35(–50) mm, villous-glandular. **Corollas** yellow with a prominent maroon blotch at the base of each lobe and white patch at the 2 sinus bases of the lower lip, weakly bilabiate to regular, sometimes nearly rotate, tube-throats cylindric-funnelform, 12–16 mm, limbs bilabiate, expanded 15–30 mm (pressed), lobes oblong-obovate to obicular-obovate, apex rounded-truncate. **Styles** glabrous. **Anthers** glabrous. **Capsules** narrowly ovoid, 4–6 mm, often slightly exserted. $2n = 32$. Map 8.

Flowering Mar–May. Steep marble outcrops in soil pockets, moss covered marble and quartzite ledges, cracks, fractures, and weathered faces, chamise chaparral or blue oak woodland; 300–1300 m; Calif. (Tulare and Fresno counties).

*Erythranthe norrisii* is known only from the Kaweah River drainage and most populations are in Sequoia National Park. The species is characterized by its short-petiolate leaves with attenuate bases, very large corollas with red blotches at the base of each lobe and two white patches on the lower lip, very short, purple-dotted calyces with rounded-thickened ribs and with linear-oblong lobes incurved in fruit. The capsules often extend beyond the apex of the mature calyces.

**Species of Asia**.

18. **Erythranthe stolonifera** (Novopokr.) Nesom, Phytoneuron 2012-39: 39. 2012. *Mimulus stolonifer* Novopokr., Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 11: 158 [with Latin] and 155 [Russian only]. 1949. **TYPE. RUSSIA**. Province Primoskaja, sinus Nachtau [Gulf of Nakhtau], 28 Jun 1911, *Dessulavi 1599* (holotype: LE).

*Erythranthe stolonifera* (Fig. 6) is endemic to the Ussuri region of Russia (Cape Olympiad, Gulf of Nakhtau, Nelka Bay; fide Novopokrovsky 1949), a coastal extension that is essentially opposite the islands of Sakhalin (Russia) and Hokkaido (Japan), bordered on the west by northeastern China and on the south by North Korea. Plants produce procumbent stems rooting at the nodes and arising from a system of lignescent rhizomes. As noted in the protologue, the plants also produce distally small-leaved runners from basal cauline nodes. The species is characterized by glandular-villous vestiture, essentially ovate, petiolate, pinnately to subpinnately veined leaves with dentate margins, long pedicels, and yellow corollas with infundibular tube-throats . It seems likely that its closest relative is the North American *Erythranthe moschata* group (*E. moschata*, *E. moniliformis*, *E. inodora*).

Figure 7. Collection of *Erythranthe stolonifera* from Primoski Province, Russia.

**Excluded species.**

*Erythranthe bridgesii* (Benth.) Nesom (Phytoneuron 2012-n: 0. 2012) was placed by Von Bohlen (1995) in the relationship of *Mimulus moschatus* and *M. floribundus*, especially based on similarities in pollen morphology and perhaps with a tacit assumption that it was related to *M. moschatus*. The placement of *E. bridgesii* within sect. *Mimulosma*, however, is problematic, especially in view of its glabrous vestiture, strongly palmately veined leaves, and truncate calyx margins. The species is tentatively placed as a continentally disjunct member of *Erythranthe* sect. *Sinopithecus* (Barker et al. 2012), with which it shares glabrous vestiture, sessile, palmately veined leaves, calyces with shallowly lobed to subtruncate margins, and broadly spreading, nearly regular corolla limbs.

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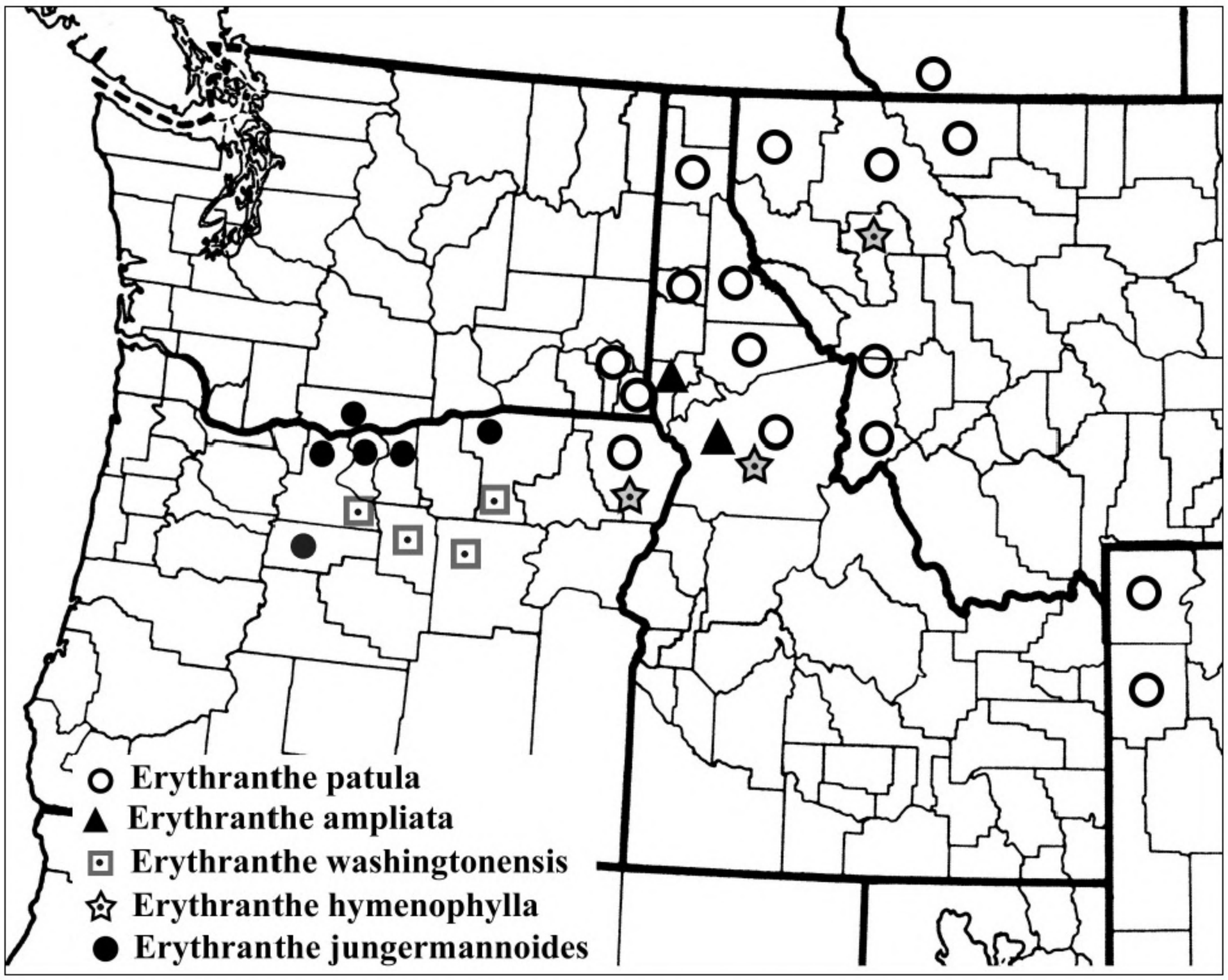
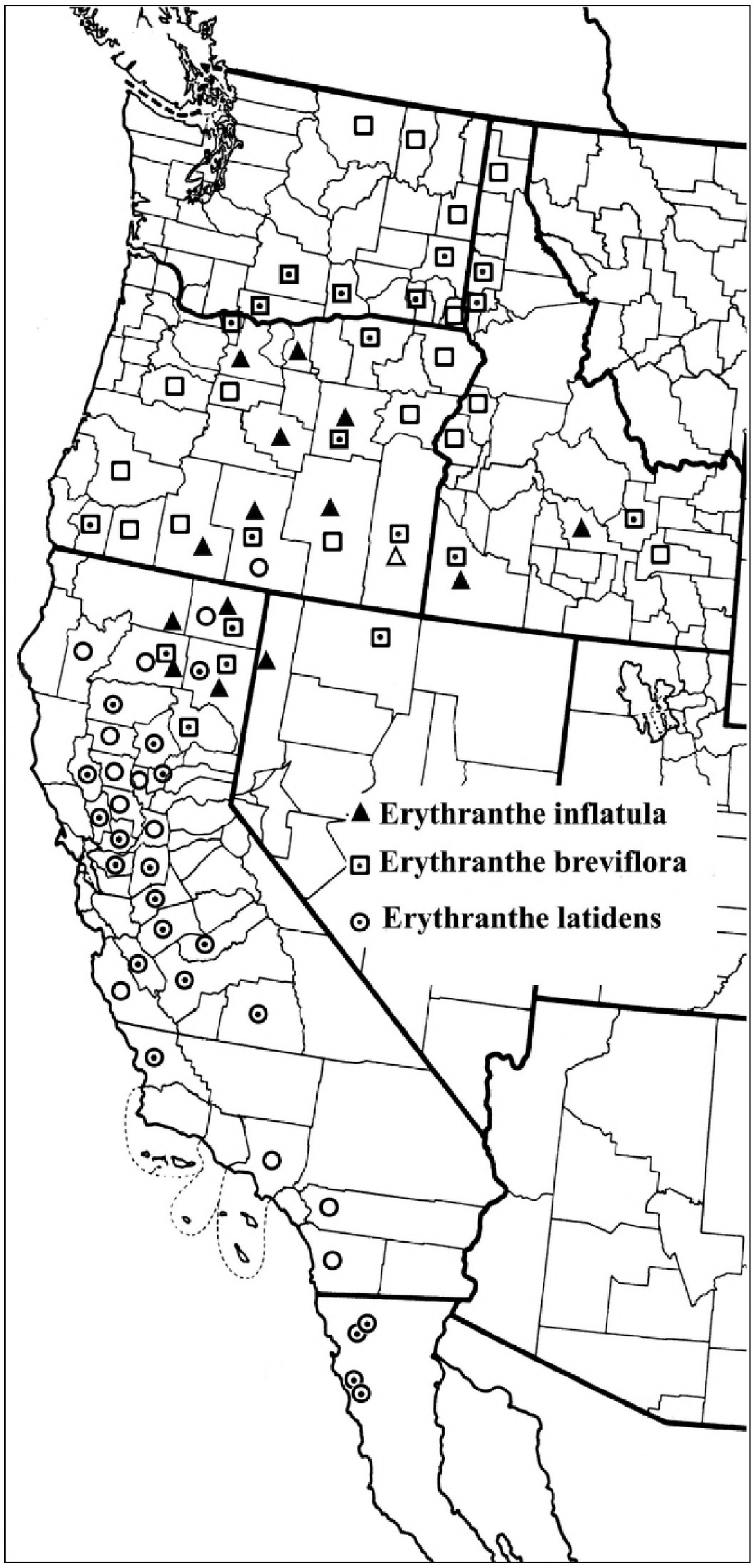
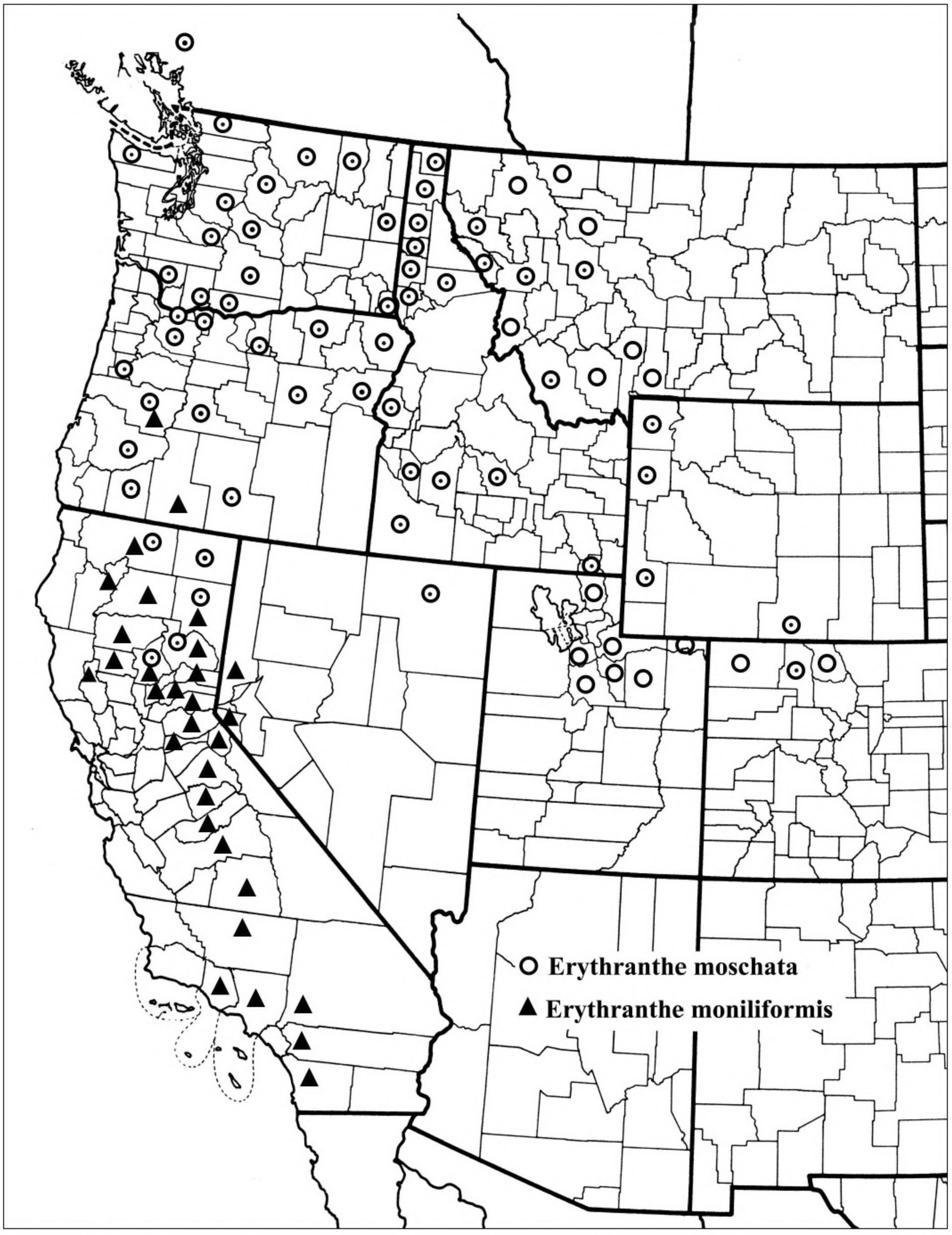



Map 1. *Erythranthe jungermannoides*, *E. washingtonensis*, *E. hymenophylla*, *E. ampliata*, and *E. patula*.

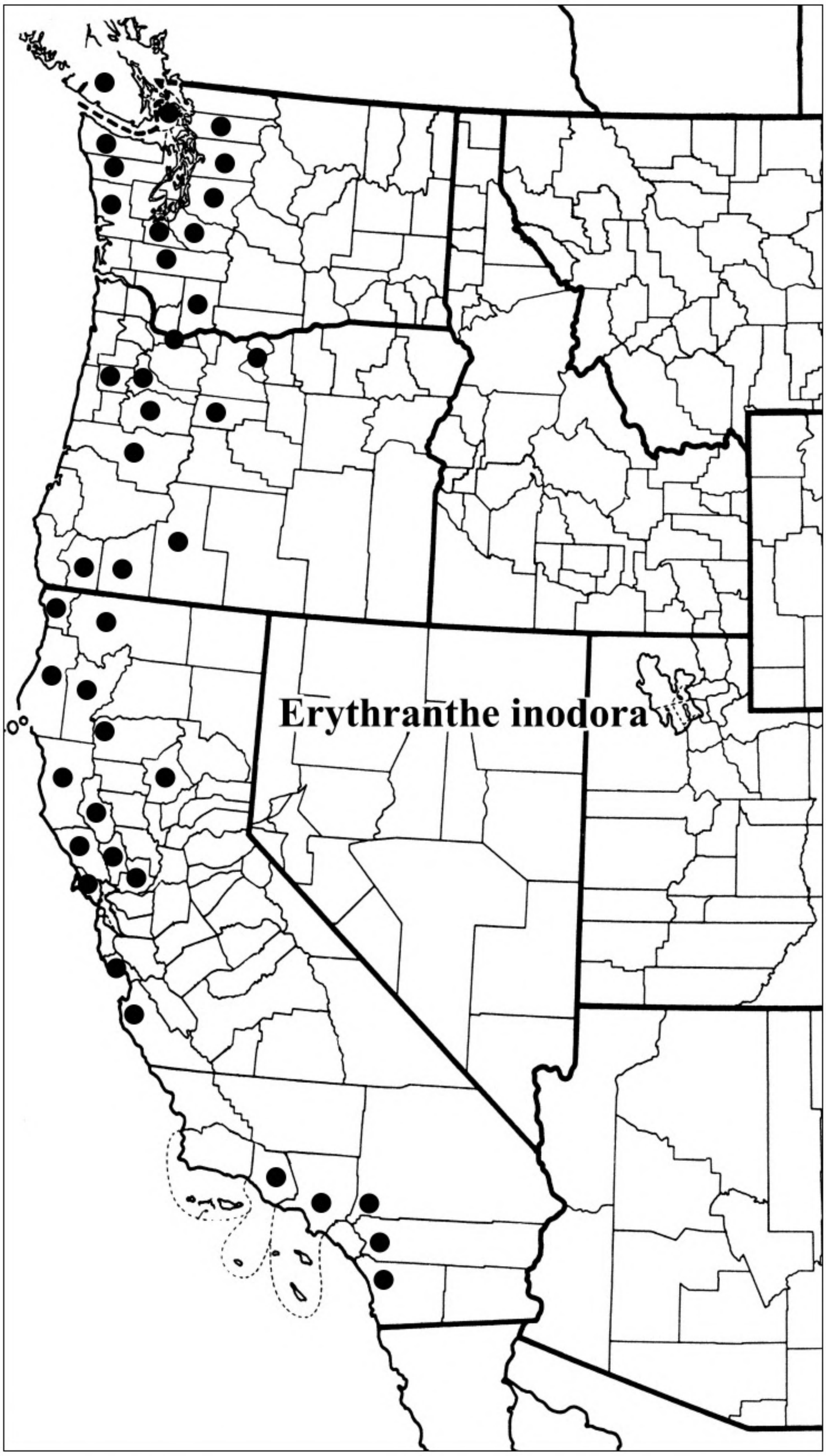



Map 2. *Erythranthe latidens*, *E. breviflorus*, and *E. inflatula*. Undotted symbols are reports from literature, vouchers not seen in present study.

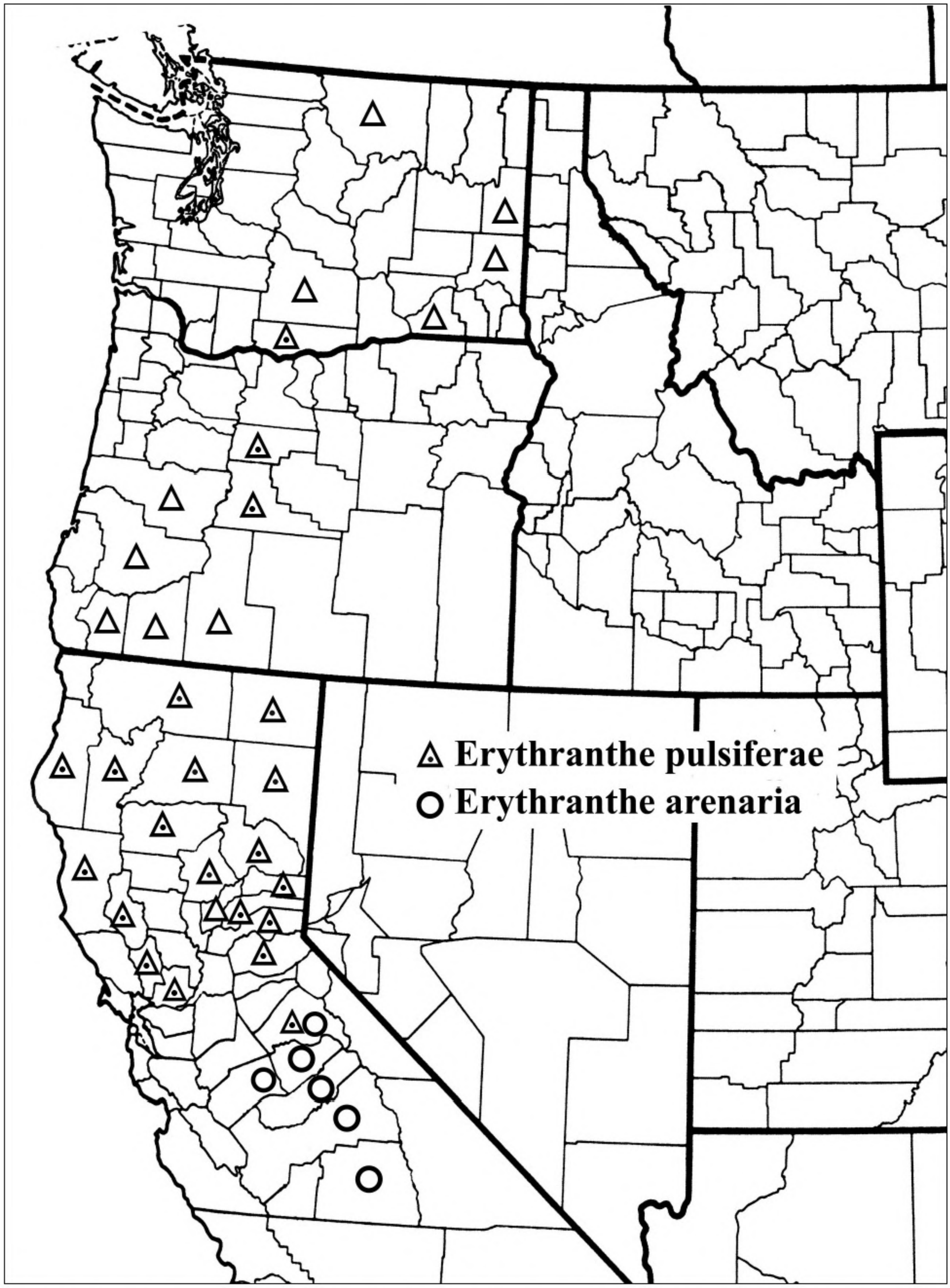
Map 3. *Erythranthe austrolatidens*.



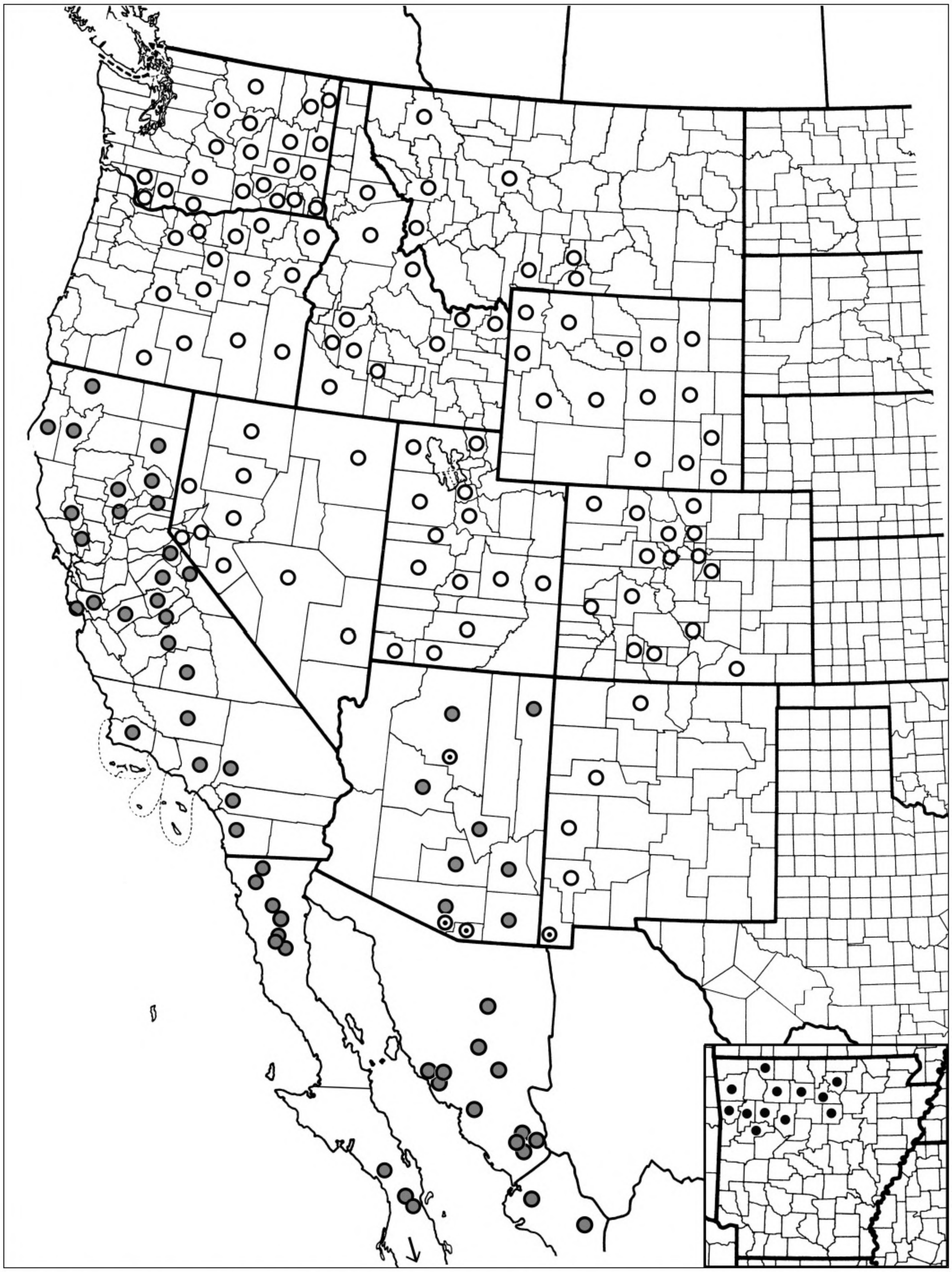

Map 4. *Erythranthe moschata* and *E. moniliformis*. Undotted circles are reports from literature, vouchers not seen in present study.



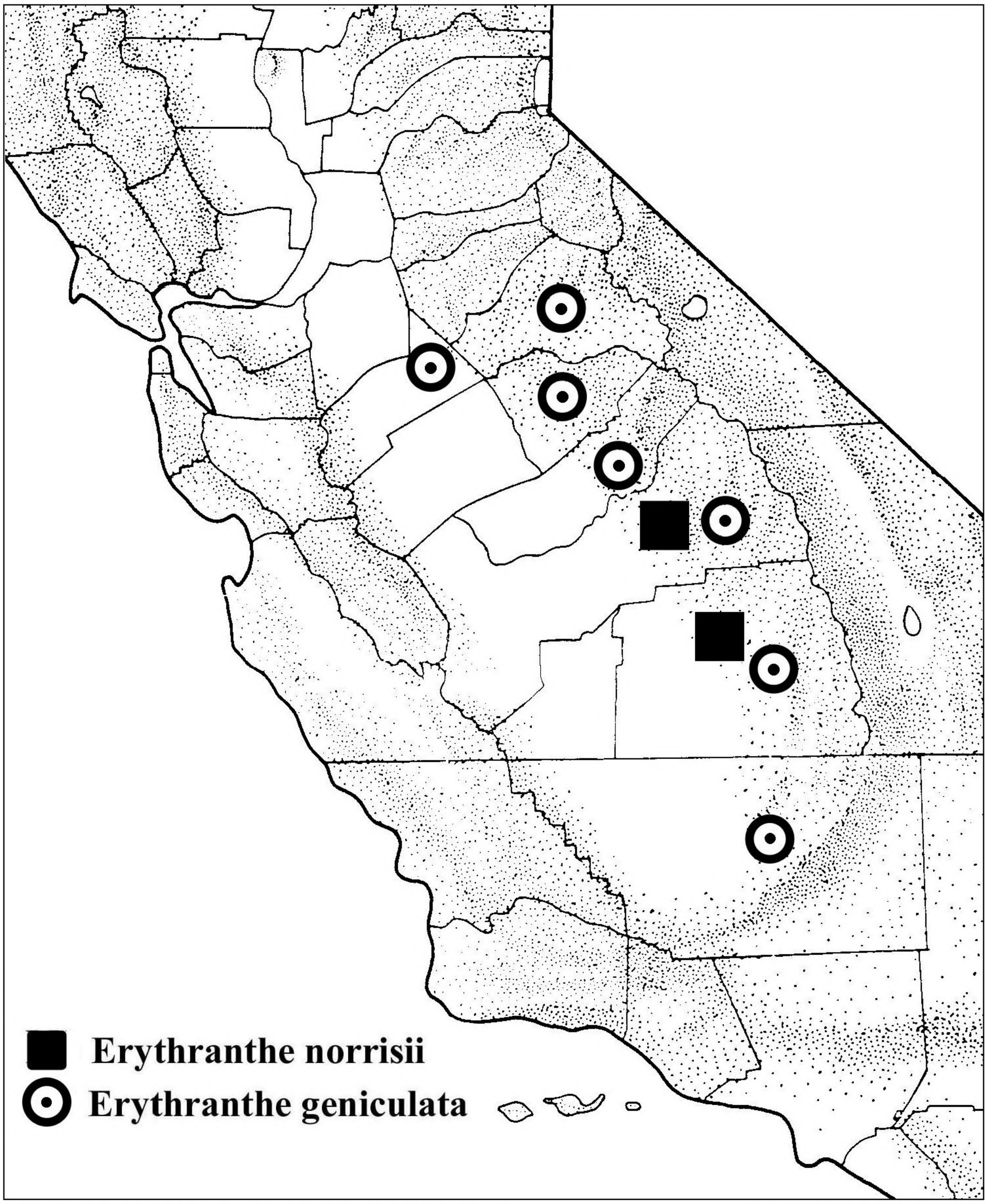

Map 5. *Erythranthe inodora.*




Map 6. *Erythranthe pulsiferae* and *E. arenaria*. Undotted symbols are reports from literature, vouchers not seen in present study.



Map 7. Distribution of *Erythranthe floribunda*. Inset show disjunct distribution in Arkansas. Dotted circles in Arizona and New Mexico are variant discussed in text. The distribution in Baja California Sur continues to the Cape Region. California records from UC-JEPS; Arizona and Mexico records are from ARIZ. TEX-LL, and SD. Other records are from various sources, vouchers seen for some but not all.




Map 8. *Erythranthe norrisii* and *E. geniculata.*